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SUBGENERIC RELATIONSHIPS IN THE EUTHECOSOMATOUS PTEROPOD GENUS *LIMACINA* BOSC, 1817.

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SUMMARY

The relationships between the species of the genus *Limacina* are examined and a new subgeneric classification based on anatomical characteristics is proposed. The subgenus *Limacina* Bosc, 1817, includes five species: *L. bulimoides* (d'Orbigny, 1836), *L. helicina* (Phipps, 1774), *L. lesueuri* (d'Orbigny, 1836), *L. retroversa* (Fleming, 1823), and *L. trochiformis* (d'Orbigny, 1836). The subgenus *Limacina* is characterized primarily by a dorsal mantle cavity, pallial gland of one cell zone, and a common pattern of reproductive morphology. Free-floating egg masses are deposited by all five species. The subgenus *Thilea* Strebel, 1908, includes a single species, *L. helicoides* Jeffreys, 1877, which has the mantle cavity offset to the right side and a pallial gland of two cell zones. The reproductive morphology of *L. helicoides* is similar to that of the subgenus *Limacina*, but encapsulated young are retained in the mucous gland of the female and the species is ovoviviparous. The subgenus *Embolus* Jeffreys, 1870, has the single species *Limacina inflata* (d'Orbigny, 1836). The reproductive morphology of *L. inflata* is substantially different from the other species of the genus; the mucous and albumen glands and the penis are absent in *L. inflata* and the prostate gland develops into a spermatophore. Females of *L. inflata* retain developing embryos in the mantle cavity where they are attached to the mantle lining.

INTRODUCTION

Euthecosomatous pteropods are a small group of opisthobranchs that are highly specialised for a holoplanktonic existence. The specialisations make it difficult to understand relationships within the Euthecosomata. For many years two families, Limacinidae Gray, 1847, and Cavoliniidae Fischer, 1883, have been recognised (Meisenheimer, 1905; Tesch, 1946; van der Spoel, 1967). In a thorough examination of the group Rampal (1973; 1975) has recently divided the Cavoliniidae into two families, Cavoliniidae sensu stricto and Creseidae Rampal, 1975. Of the three euthecosome families the Limacinidae are considered to be the most primitive (Tesch, 1946; van der Spoel, 1967; Rampal, 1975).

The family Limacinidae has a single genus, *Limacina* Bosc, 1817 with seven widely distributed species. *Limacina helicina* (Phipps, 1774) is a polar species and *L. retroversa* (Fleming, 1823) is a temperate species. Both are bipolar, occurring in the northern and southern hemispheres with distributional gaps in the equatorial regions. Four species are distributed throughout the tropical and subtropical oceanic regions: *L. bulimoides* (d'Orbigny, 1836), *L. inflata* (d'Orbigny, 1836), *L. lesueuri* (d'Orbigny, 1836), and

L. trochiformis (d'Orbigny, 1836). All six of the above species are epipelagic. The only bathypelagic member of the genus, *L. helicoides* Jeffreys, 1877, has been recorded from the North and South Atlantic and the South Pacific Oceans (van der Spoel, 1967).

Although the species are well known the genus *Limacina* has been divided into a confusing array of subgenera. The most recent attempt to establish relationships within the genus was that of van der Spoel (1967). Three subgenera were recognised primarily on the basis of shell shape: *Limacina* Bosc, 1817, with *L. helicina* and *L. retroversa*; *Thilea* Strebel, 1908, with *L. inflata*, *L. lesueuri* and *L. helicoides*; and *Munthea* van der Spoel, 1967, with *L. bulimoides* and *L. trochiformis*. In her excellent examination of the euthecosome fauna of the Mediterranean Sea, Rampal (1975) has discussed reasons for removing *L. helicoides* from the genus *Limacina*, and placing it in the genus *Thilea* Strebel, 1908.

The reproductive mechanisms and morphology of all seven species have now been investigated (Lalli and Wells, 1973; Wells and Lalli, in prep.). This work has shown *L. inflata* to have brood protection and a reproductive anatomy unlike that of other species of *Limacina*. This information on reproduction should be incorporated into our understanding of relationships between the various species, and the subgeneric classification of *Limacina* should be modified accordingly.

DISCUSSION

(a) General *Limacina* pattern

Table 1 summarises the published information which can be used to indicate relationships between the various species of *Limacina*. Five species: *L. bulimoides*, *L. helicina*, *L. lesueuri*, *L. retroversa* and *L. trochiformis*, all fit into one grouping. These species are united by the following characteristics: mantle cavity dorsal, parapodia well developed, pallial gland of one cell zone, 'balancer' or excurrent siphon¹ in the right angle of the mantle cavity and epipelagic habitat. All species deposit free-floating egg masses, and there is a common reproductive morphology.

The general pattern of the reproductive system of *Limacina* is as follows. The hermaphroditic gonad is located in the upper shell whorls, and a hermaphrodite duct leads from the gonad to the albumen and mucous gland. The prostate gland is located at the base of the penis. All species are protandric hermaphrodites. During the male stage the lower portion of the gonad and hermaphrodite duct are swollen by endogenous sperm. After copulation has occurred exogenous sperm are stored in the hermaphrodite duct. During copulation sperm move through the common genital pore, along a ciliary tract on the right side of the head, and onto the penis. During the female stage free-floating egg masses are laid (Wells and Lalli, in prep.).

However, there are also three characters on Table 1 which appear to separate the species: presence or absence of a tentacular lobe on the anterior surface of the parapodia, height of the shell spire and type of shell structure. The five species are spread over all three subgenera proposed by van der Spoel (1967), but Rampal (1975) believed there was no need to subdivide the group. The presence or absence of a tentacular lobe is a minor characteristic which varies even within the species *L. helicina*. The shape of the shell spire varies within the species *L. retroversa* (Tesch, 1946) and in *L. helicina* (McGowan, 1963). Microscopic shell structure varies within the species *L. helicina* and *L. bulimoides* (Rampal, 1975).

1. The use of the term 'balancer' originated with Pelseneer (Rampal, 1975). Pelseneer, working with preserved material from the Challenger Expedition, suggested the coiled shells of *Limacina* would be unstable while the animals were swimming. The 'balancer' was thought to provide stability in the water column. In fact the animals are unable to travel in a straight line and swim upwards in a spiral path as described by Morton (1954a). Boas found the 'balancer' to function in evacuating the mantle cavity in the pseudothecosome genus *Peractis* (cited in Rampal, 1975). I have examined live animals of all three euthecosome families collected in a two year sampling program off Barbados (Wells, 1976). In all species examined the 'balancer' served to channel water out of the mantle cavity without an apparent stabilising function. The structure should be regarded as an excurrent siphon, and not a 'balancer'.

Thus these five species of the genus *Limacina* should be regarded as belonging to a single subgenus *Limacina* Bosc, 1817, with the characteristics outlined in the first paragraph of this discussion. *Limacina helicina* (Phipps, 1774) is the type species of the genus.

(b) *Limacina helicoides*

Limacina helicoides differs from the other members of the genus in the following characteristics: the mantle cavity is offset to the right side, the parapodia are not as well developed as in the other species, the pallial gland has two cell zones, and the excurrent siphon is in a slightly different position. All of these characters clearly separate *L. helicoides* from the subgenus *Limacina*. Rampal (1975) cited two additional differences: *L. helicoides* is the only bathypelagic member of the genus and it is ovoviviparous. As Tesch (1946) has observed, bathypelagic species are often ovoviviparous. Three cavoliniids of the genus *Clio* are known to have embryo retention and all are bathypelagic (Lalli and Wells, 1973). The reproductive morphology of *L. helicoides* does not differ from that of the subgenus *Limacina*. Encapsulated embryos are simply retained in the mucous gland of the female during development (Wells and Lalli, in prep.). *Limacina helicoides* can certainly be differentiated from the other species of the genus, but the differences do not warrant a generic separation. The subgenus *Thilea* Strebel, 1908, should be used for this species.

Three of the characteristics on Table 1 are used by Rampal (1975) in assessing the evolutionary relationships of the euthecosomes: position of the mantle cavity, cellular structure of the pallial gland, and location of the excurrent siphon. In all three characteristics Rampal believes *L. helicoides* shows a more primitive structure than the other Limacinidae and the Creseidae and Cavoliniidae.

(c) *Limacina inflata*

As is shown on Table 1, *Limacina inflata* shares many characteristics of the subgenus *Limacina*, such as the dorsal mantle cavity, position of excurrent siphon, well developed parapodia, pallial gland of one cell zone and epipelagic habitat. The substantial differences separating *L. inflata* from the other species lie in the method of reproduction. Developing embryos are retained attached to the mantle lining of the female and young are released as free-swimming veligers (Lalli and Wells, 1973). The reproductive morphology is marked by the loss of the albumen and mucous glands and the penis. The prostate gland is elaborated into a spermatophore for sperm transfer and is directly connected by the hermaphrodite duct to the gonad. The direct link between the prostate and gonad has not been reported in any other thecosome (Wells and Lalli, in prep.). The reproductive modifications of *Limacina inflata* can be used to clearly separate the species at the subgeneric level. I suggest using the subgenus *Embolus* Jeffreys, 1870, for *Limacina inflata*, as it was used by Johnson (1934).

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WELLS, F E. and C M LALLI' Reproduction in thecosomatous pteropod genus *Limacina*. In prep.

TABLE 1. Characteristics of *Limacina* species

Structure	Subgenus <i>Limacina</i>		Subgenus <i>Thilea</i>		Subgenus <i>Embolus</i>		Source
	<i>L. bulimoides</i>	<i>L. helicina</i>	<i>L. lesueurii</i>	<i>L. retroversa</i>	<i>L. trochiformis</i>	<i>L. helicoides</i>	
Position of mantle cavity.	Dorsal	Dorsal	Dorsal	Dorsal	Right lateral	Dorsal	Rampal, 1975.
Parapodia	Well developed	Well developed	Well developed	Well developed	Poorly developed	Well developed	Rampal, 1975.
Habitat	Epipelagic	Epipelagic	Epipelagic	Epipelagic	Bathypelagic	Epipelagic	Wells and Lalli, in prep.
Pallial gland	One cell zone	One cell zone	One cell zone	One cell zone	Two cell zones	One cell zone	Rampal, 1975.
Excurrent siphon	Right corner of mantle cavity	Right corner of mantle cavity	Right corner of mantle cavity	Right corner of mantle cavity	Offset of mantle cavity	Right corner of mantle cavity	Rampal, 1975.
Reproductive mechanisms	Oviposition	Oviposition	Oviposition	Oviposition	Ovoviviparity	Brood protection	Lalli & Wells, 1973. Wells & Lalli, in prep.
Reproductive morphology	Typical	Typical	Typical	Typical	Typical	Modified	Wells & Lalli, in prep.
Tentacular lobe	Absent	Present or absent	Absent	Present	Absent	Absent	van der Spoel, 1967.
Shell spire	Normal	Flattened	Flattened	Normal	Flattened	Flattened	van der Spoel, 1967.
Shell structure	Prismatic and cross-lamellar	Prismatic and cross-lamellar	Cross-lamellar	Cross-lamellar	Cross-lamellar	Prismatic	Boltovskoy, 1975; Rampal, 1975.
Distribution	Tropical	Polar	Tropical	Tropical	Bathypelagic	Tropical	van der Spoel, 1967.

RECORDS OF *PHILINOPSIS LINEOLATA* (H. & A. ADAMS, 1854) (OPISTHOBRANCHIA:AGLAJIDAE) FROM SOUTH-EASTERN AUSTRALIA

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Philinopsis lineolata (H. & A. Adams, 1854), originally described from Australia, has since been recorded from Thailand (Bergh, 1902), the Andaman Islands (White, 1945), and Japan (Baba, 1949). Very recently, the species was recorded again from Australia, and figured in colour (Coleman, 1975: 181). The figured specimen, now in the National Museum of Victoria, has the following data: Heron Island, Queensland, on sand at low tide, 22 July 1973, coll. Neville Coleman, 1 specimen (F30102).

P. lineolata occurs also in Victoria and New South Wales, giving the species a wide distribution along the eastern coast of Australia.

Off Limeburners Point, Corio Bay, Port Phillip. 2.6 m on sandy-mud, 16 May 1963, coll. J.H. Macpherson & party, 1 specimen preserved length 27 mm (F26012). As preserved, the body is a very dark brown colour with numerous transverse extremely narrow lighter lines on the head, visceral hump and parapodia. The penis, the tip unfortunately severed during examination, has the usual row of fleshy papillae along one edge. This specimen was formerly misidentified by the writer and reported twice as *Aglaja cyanea* (Martens, 1879) (Burn, 1966: 267; 1969: 73).

Mud Island, Port Phillip, Victoria, 7 m on sand, 18 February 1978, coll. D. Staples, 1 specimen preserved length 24 mm (F3 0103). In life, the specimen was a very dark brown with numerous transverse narrow lighter lines, some of which at the margins of the head and parapodia widen to form shining white stripes. The penis has the usual row of fleshy papillae. As preserved, it agrees exactly with the Limeburners Point specimen.

Fly Point, Port Stephens, New South Wales, 15 m on sand, 27 February 1977, coll. Neville Coleman, 1 specimen preserved length 10 mm (F30104). In life, the specimen was dark brown laterally and lighter brown dorsally, with prominent transverse narrow lighter, almost white, lines, some of which in the median line and at the margins of the head and parapodia widen to form distinctive white stripes. The anterior pedal margin and the posterior lobes are deep blue in colour.

South Coogee, Sydney, New South Wales, 19 February 1978, coll. R. & A. Kuiter, 1 specimen (Australian Museum C108933), identified from colour slides. In life, animal coloured precisely as the specimens from Port Phillip, Victoria.

Although these specimens are all identified with *P. lineolata*, they can be separated into two forms. The tropical form is lighter in colour with blue pigment on the anterior pedal margin and the posterior lobes; the Heron Island and Port Stephens specimens, and the Thai, Andamanese and Japanese records belong to this form. The temperate form is much darker in colour and has no blue pigment; the Port Phillip and Coogee specimens are this form.

The use of the genus *Philinopsis* Pease (1860) follows the recent studies by Rudman (1972, 1974).

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ZONITOIDES ARBOREUS (SAY) (PULMONATA : ZONITIDAE) INTRODUCED
INTO AUSTRALIA AND THE IDENTITY OF *ALIENITOR* IREDALE.

M. J. BISHOP

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Receipt of a zonitoid snail for identification from glasshouses at Ormiston, Queensland (MO6050) and the discovery of the same species living in a garden in Brisbane City (MO6051) has prompted publication of the following note.

The shell is translucent light brown, about 2.4 mm high and 4.8 mm wide, umbilicate with 4½ whorls. The animal is coloured blue-grey with paler flecks the foot having two pedal grooves. On dissection, the genitalia prove to be most complicated with a dart sac arising from the base of the penis. The dart sac has a bifurcate coronal gland and attaches to the duct of the bursa copulatrix which also has a diverticulum attaching to the penis sheath.

The subfamily Gastrodontinae of the Zonitidae is immediately suggested and no difference could be observed between the genitalia figured by Pilsbry (1946: fig. 258F) for *Zonitoides arboreus* (Say) and the genital anatomy of the Queensland material. This species has been introduced from North America to many parts of the world and Pilsbry lists an Australian record from Vancluse (error = Vaucluse), N.S.W. a suburb of Sydney.

Turning to the Australian literature (Cotton, 1954) we find no mention of *Z. arboreus* although *Z. nitidus* (Müller) is listed. Long (1972) considered that records of *Z. nitidus* from Australia probably represented specimens of *Oxychilus alliarius* (Miller). I consider that some records of *Z. nitidus* could represent *Z. arboreus* so that there is no adequately authenticated record of *Z. nitidus* from Australia.

Examination of the holotype of *Helix lyndhurstensis* Cox (1868: 11, pl.17, fig.1) in the Australian Museum (C227, broken) from Lyndhurst, N.S.W. indicates that this too is *Z. arboreus*. Iredale (1937: 6) introduced the genus name *Alienitor* for this species commenting "a small Zonitid of distinct appearance, recalling extra-limital forms". McLaughlan (1954: fig 3) dissected material he identified with *Alienitor lyndhurstensis* (Cox) from Glebe, Sydney, N.S.W. His figure of the anatomy is sufficient to show that the material was *Z. arboreus*. He may have recognised this himself for he states "Apparently developed from an introduced form of *zonitoides* (sic)". He also described a supposed new species, *Alienitor lyndhurstoides* McLaughlan (1954: 40, fig 4) from Clifton Gardens, Sydney, N.S.W. and examination of the five syntype shells (AM C101178) proves that they are also *Z. arboreus*. This is borne out by his figure of the anatomy, supposed differences from *A. lyndhurstensis* being attributable to individual variation. McLaughlan (1954) states that *A. lyndhurstensis* is common from Queensland to Victoria but Long (1972) makes no mention of *Z. arboreus* in the latter State.

To conclude, *Zonitoides arboreus* is introduced into Australia in Queensland and New South Wales. The presence of *Z. arboreus* in Victoria has not been confirmed after examination of a large quantity of preserved zonitid material in the National Museum of Victoria. I have not considered it necessary to figure Queensland material as McLaughlan's figures are adequate to confirm the presence of the species in Australia and Pilsbry's work is ideal for identification. Burch (1976) listed *Alienitor* in the subfamily Microcystinae of the Euconulidae. The taxonomic conclusions from this study are

that *Alienitor* Iredale is a junior synonym of *Zonitoides* Lehmann. *Helix lyndhurstensis* Cox and *Alienitor lyndhurstoides* McLaughlan are junior synonyms of *Zonitoides arboreus* (Say).

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A REVISION OF THE GENUS *THERSITES* PFEIFFER (PULMONATA : CAMAENIDAE)

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SUMMARY

Camaenid land snails do share some derived anatomical features and the family should not be characterised in negative terms. The genus name *Thersites* was formerly employed for a large number of Australian camaenids but should be restricted to include only *T. mitchellae* (Cox), *T. novaehollandiae* (Gray) and *T. richmondiana* (Reeve). *Thersites* is characterised by the possession of granular shell sculpture, a dorsal cream coloured line on the neck, a curious bend in the duct of the bursa copulatrix and a large imperforate conical papilla in the penis.

"The appreciation of that indefinable something, which counts for so much in classifying *Helices* ... this accurate feeling for subtle affinities for which no good reason can be given in words" (Pilsbry 1895: xxii)

INTRODUCTION

The presently accepted classification of the Australian camaenid land snails (Iredale, 1937-38; Burch, 1976) is based almost entirely on shell characters and is largely unworkable. The larger, richly coloured shells of coastal eastern Australia have long been known, but great confusion has always existed, both as to the number of individual species, and to the limits of the genera into which they should be placed. This paper represents the first part of a taxonomic revision of these animals which will attempt to elucidate their phylogenetic relationships and to place their classification on a firmer basis.

FAMILY CAMAENIDAE

Helicoid land snails were originally recognised as a distinct group on the basis of their shell shape and texture. Pilsbry (1895) introduced a new classification of *Helices* and urged that a natural classification should be based on the consideration of all the organ systems and not upon the shell alone. He divided the "*Helicidae*" into the subfamilies Polygyrinae, Acavinae, Camaeninae and Helicinae. Apart from the removal of the Acavinae to other places and the upgrading in rank of the taxa, his classification is still recognisable in the most recent compilation by Taylor and Sohl (1962).

The only distinction between the Polygyrinae and the Camaeninae in Pilsbry's diagnosis (1895: xxxii) is that the former were supposed not to possess an epiphallus or flagellum. Later work

(Pilsbry 1940: 575) has shown that this is not always the case. The Camaenidae were characterised thus: genitalia without accessory appendages on the female side; no diverticulum of the duct of the bursa copulatrix; small and numerous eggs; solid smooth or ribbed jaw; radula teeth primitively tricuspid with squarish base plates; shell usually solid, the lip expanded or reflexed. These characters are possessed not only by the Camaenidae but by many other members of the Stylommatophora. We are left with the feeling that certain shell characters, too subtle to express, are the only derived features of the family, and that anatomy has been of little use other than to weed out forms which are clearly not camaenids.

The Camaenidae tended to become a dumping ground for sigmurethran land snails with helicoid shells until Wurtz (1955) pointed out some derived features possessed by the family: the bunches of alveoli in the ovotestis are coalescent; the kidney is primitively at least ten times as long as wide; the kidney is three to four times the length of the pericardium; the left parietal ganglion is fused with the visceral ganglion. Wurtz showed that these features are not shared by the Ammonitellinae (= Megomphicinae) and the Oreohelicinae and that these groups should have separate family status. The Megomphicinae and the Oreohelicinae each have distinct advanced features of their own and cannot be considered as antecedents to the Camaenidae. There is no phylogenetic reason to group the three families in superfamily Camaenacea.

Solem (1973) described the anatomy of the Queensland land snail *Craterodiscus* and assigned it to the "Camaenidae s.l.". In doing so he relied largely upon negative evidence and shared primitive characters, dismissing a large range of sigmurethran taxa as having more advanced character states, before reaching his conclusion. He explained the different pallial configuration as derived from the camaenid state. We do not have information on the jaw and central nervous system, so *Craterodiscus* is only doubtfully a member of the Camaenidae.

Here I am describing a genus which is undoubtedly a member of the Camaenidae for it agrees in all those characters enumerated for the family by both Pilsbry and Wurtz.

GENUS *THERSITES* PFEIFFER (1855)

Type species: *Helix richmondiana* Reeve (1852) by subsequent designation of Martens (1860).

Synonym: *Annakelea* Iredale (1933) new name for *Thersites* with the same type species. When introducing *Annakelea*, Iredale rejected Martens designation stating: "the tautonymic type of *Thersites* must be *H. thersites* Broderip. The latter is not an Australian form at all, so *Thersites* must be dismissed from Australian malacological study". Iredale's view is not upheld and Martens designation is accepted (Zilch 1959-60).

Diagnosis: Eastern Australian camaenid land snails; shell at least 25 mm in width, often keeled, with granular sculpture; there is a light coloured line running between the dorsal grooves on the neck; the seminal receptacle is not extended as a talon beyond the point of entry of the hermaphrodite duct; the duct of the bursa copulatrix has a bend about 1/3 - 1/2 of the way from its junction with the oviduct; the epiphallus bears a flagellum with a pointed tip; a large imperforate conical papilla occupies more than half the length of the cavity of the penis.

History of the genus: Pilsbry (1890: 90) first included only *H. richmondiana* Reeve and *H. novae-hollandiae* Gray in *Thersites*, placing the other large eastern Australian camaenids, including *H. mitchellae* Cox, in *Hadra*. He later (1895: 127) considered that *Thersites* and *Hadra* were congeneric and that *Thersites* would have to be used as the genus name for the whole group, in which he recognised *Thersites*, *Xanthomelon* and *Rhagada* as subgenera. Within the subgenus *Thersites* he recognised the sections *Thersites*, *Glyptorhagada*, *Badistes*, *Hadra* and *Sphaerospira*. He assigned *H. mitchellae* to the last of these. Pilsbry received a specimen of *H. mitchellae* from Dr. Cox and discovered that the species possesses a swollen penis containing a large stimulator, and a curious bend in the duct of the bursa copulatrix. This was so much like the condition in *H. richmondiana* figured by his friend Charles Hedley (1889: 62, pl.3) that Pilsbry concluded that *Thersites* and *Sphaerospira* are indistinguishable from the anatomical point of view. In this Pilsbry was wrong, as he did not have the opportunity to examine the type of *Sphaerospira*. *H. fraseri* Griffith and Pidgeon. Had he done so, he would have found that the genital anatomy of *Sphaerospira*

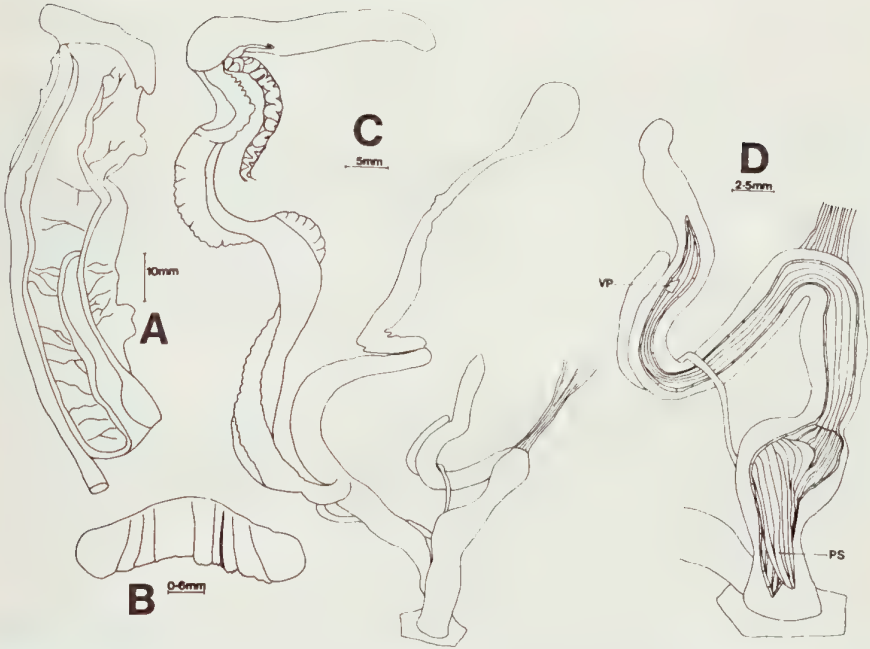


FIGURE 1. *Thersites richmondiana* (Reeve), Binna Burra, Lamington National Park, Queensland. (QM). A-pallial complex, B-jaw, C-reproductive system and D-penial complex. (PS penial papilla, VP vas papilla.)

is quite distinct from that of *Thersites* (Bishop, in press). For this reason Pilsbry's account is somewhat confused and Burch's (1976: 146) reference to Pilsbry's fairly careful study is not entirely justified.

Fulton (1904) realised that Pilsbry was mistaken about the affinities of *H. mitchellae* and placed the species in the section *Thersites*. Iredale (1933, 1937-8) was dissatisfied with Pilsbry's treatment and felt that many more family and generic units were represented within the genus *Thersites* than had been allowed. The cursory nature of the descriptions with which Iredale introduced his new taxa are legendary, and this has led to the suspicion that many may be nomina nuda (Solem, 1964), though this has been denied (McMichael, 1964). No further anatomical evidence being available, Zilch (1959-60) followed Pilsbry's treatment of the group, with some changes in rank.

Shell: The shell of *Thersites* is large and solid, at least 15 mm in height and 25 mm in width. The shape is variable according to species. The umbilicus is open in juvenile specimens but closed in the adult. There are $5\frac{1}{2}$ - 6 whorls and a brown periostracum with granular sculpture (Fig. 4C-E). The shell is marked with chestnut and yellow-brown bands, light on the keel and dark below the suture, above the keel and around the umbilicus. The width of the bands is variable so that shells may appear yellow with brown lines or brown with yellow lines. A common form of *T. richmondiana* is entirely dark brown. The peristome is thick, expanded, reflexed and glossy dark brown and may be sinuous and somewhat toothed.

Anatomy: External appearance of the animal is not distinguishable from *Sphaerospira* (Bishop in press) except that the dorsal grooves on the neck are somewhat more prominent with a light coloured line between them. There is no keel on the back, and the collar has the usual left and right body lobes.

The pallial complex is sigmurethrous with the gut ureter closed all the way to the collar (Fig. 1A). Delhay & Bouillon (1972) were wrong to attribute an open secondary ureter to *Thersites* as "*T. meridionalis*" (Brazier) is not a member of the genus. The kidney is very long and narrow, being ten times as long as broad, half the length of the lung roof and three and a half times the length of the pericardium. The apical angle of the lung does not extend beyond the kidney.

The free retractor muscles have the same pattern as *S. fraseri*, the buccal, and left and right compound retractors all being separately inserted at the columella. The right ocular retractor passes between the penis and the vagina.

The jaw is strong and ribbed (Fig. 1B, 2, 3A), though the width of the ribs is somewhat irregular. The radula teeth (Fig. 2, 4A-B) are unicuspid except for the marginals which have a long bicuspid inner tooth and a small ectocone which may be further divided according to Pilsbry (1895: 126). The salivary glands are fused over the oesophagus. The crop and stomach present the same internal appearance as in *S. fraseri*: there is a short crop fold running to the entrance of the duct of the anterior part of the digestive gland, a longer crop fold arises sooner and runs to the posterior opening; there is a small triangular accessory fold and the usual typhlosoles are present.

The ganglia of the visceral chain are concentrated and the left parietal ganglion is fused with the visceral ganglion.

The ovotestis is embedded in the digestive gland and consists of five coalescent lobes with numerous ovoid alveoli. The hermaphrodite duct is much convoluted along the middle part of its length. It enters the seminal receptacle-fertilisation pocket complex at the posterior so there is no projecting talon (Fig. 4F). The albumen gland and spermoviduct are like those of *S. fraseri*. The bursa copulatrix is attached to the spermoviduct with connective tissue. The bursa duct is very long with a curious bend about one third to one half of the way from the oviduct (Fig. 1C, 2, 3B). The vagina is bound to the adjacent body wall with tough fibres. The penial complex is enclosed in a thin sheath and has a flagellum with a pointed tip. The proximal part of the epiphallus before the point of insertion of the retractor muscle is indistinguishable internally from the distal part. Flagellum, epiphallus and penis are all lined with fairly even longitudinal corrugations. The penis contains a large imperforate conical papilla which has a longitudinally grooved surface (Fig. 1D, 3C).

Functioning of the penis was studied in an animal of *T. richmondiana* narcotised by injection of nembutal and dissected under saline. A swollen brown coloured atrial disc appears. The penis is everted and the distal part of epiphallus is extruded within it until the retractor muscle reaches the body wall. The basal part of the extruded penis is soft and flexible; towards the orifice it is bulging and corrugated. The papilla forms an extension of the penis with the orifice at its base and a deep groove runs up from the orifice towards the tip of the papilla (Fig. 5). A copulating pair has not been examined and it is not known if spermatophores are exchanged. The length of the vagina is such that the orifice of the extruded penis cannot be brought as far as the opening of the oviduct. The groove in the papilla probably acts to direct sexual products to the base of the bursa duct. The length of the intromittent organ is such that this is possible and the swollen upper region of the penis may help to hold the penis within the vagina.

KEY TO THE SPECIES OF *THERSITES*

1. a. Adult shell almost as high as wide
(ratio $> 0.8:1$) *mitchellae* (Cox)
- b. Adult shell considerably less high than wide
(ratio $< 0.7:1$) 2
2. a. Flagellum short ($\frac{1}{4}$ the length of the proximal part of the epiphallus) and hooked (Fig. 3C)
..... *novae-hollandiae* (Gray)
- b. Flagellum longer ($\frac{1}{2}$ the length of the proximal part of the epiphallus) and straight (Fig. 1D)
..... *richmondiana* (Reeve)

THERSITES MITCHELLAE (COX)

FIG. 2; 4C; 8-10

Helix mitchellae Cox, 1864 : 19.

Type locality: Clarence River.

Location of type: not traced in the Australian Museum (AM).

Synonym: *Annakelea peragrans* Iredale, 1937: 37, pl.3, Fig. 22. Type locality: Bangalow, Byron

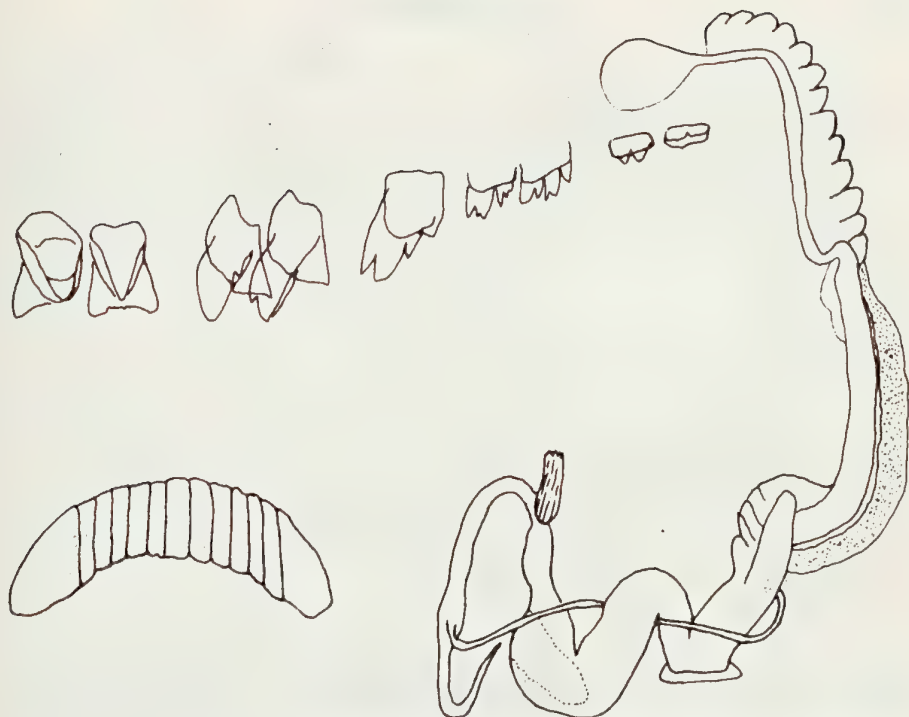


FIGURE 2. *Thersites mitchellae* (Cox). Radula teeth, jaw and distal genitalia. (After Pilsbry).

Bay. Location of type: AM C100663. Iredale considered *H. mitchellae* angulate at the periphery, whereas his new species was not. Examination of a series of specimens shows that there is a transition between the two states.

Diagnosis: The shell is large (40 mm high) and elevated (height:width 0.9:1); angulation of the periphery is weak or absent. Shell sculpture consists of closely packed granules (Fig. 4C). The flagellum is about as long as the proximal part of the epiphallus (judging by Pilsbry's figure, Fig. 2).

Distribution: (Fig. 6). New South Wales 28° 30'S 153° 30'E Ballina (AM), Bangalow (AM), Broken Head (AM), Byron Bay (AM), Eminigrant Ck. (AM), Tweed River (QM); "Richmond River" (AM); "Clarence River" (AM).

This species has not been collected for over fifty years and the only preserved animal in existence is probably that examined by Pilsbry and housed in the Academy of Natural Sciences, Philadelphia. The species occurred in the southern part of the range of *T. richmondiana* but had a more lowland and coastal distribution. The rain-forests where the species probably occurred have largely been destroyed, but a search for living colonies would be worth while.

THERSITES NOVAEHOLLANDIAE (GRAY)

FIG. 3; 4B, D; 11-13

Carocolla Novae Hollandiae Gray, 1834: 67.

Type locality: in Nova Hollandia, 200 millia passuum ab Ostio Fluvii Macquarrie. Subsequently designated as Scone, New South Wales by Iredale (1937).

Location of type: not traced in the British Museum (BM).

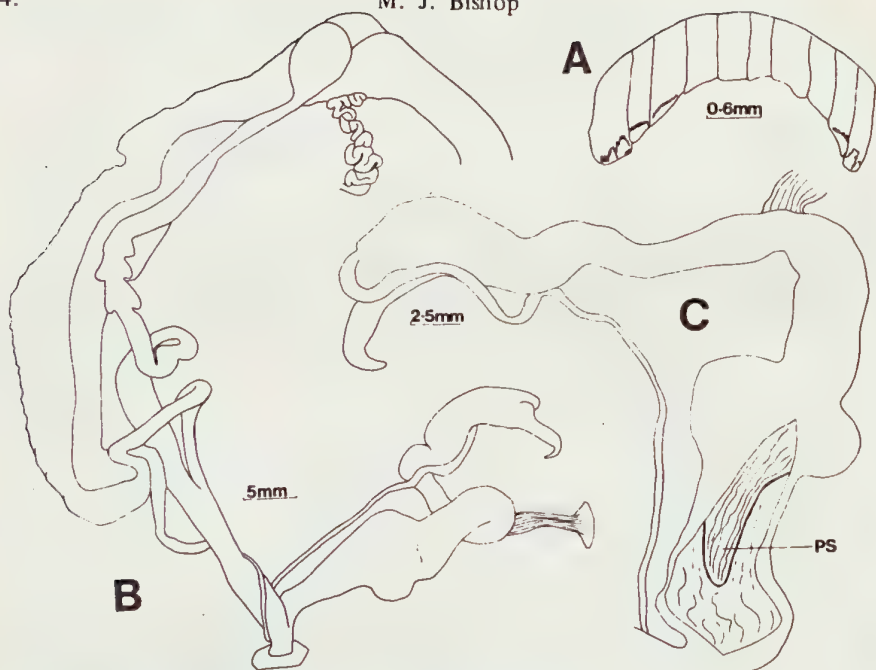


FIGURE 3. *Thersites novaehollandiae* (Gray), Dorrigo State Park, New South Wales (AM). A-jaw, B-reproductive system, C-penial complex. (PS penial stimulator.)

Synonyms: *Helix Dupuyana* Pfeiffer, 1851: pl. 124, fig. 15-16. Type locality: Ostkuste von Neuhoolland. Location of type: BM 197732 (2 syntypes). In his description Pfeiffer made no reference to the *C. novaehollandiae* of Gray.

Diagnosis: The shell is usually small (20 mm high) and depressed (height:width 0.6:1) with an angulate periphery. Shell sculpture consists of scattered granules with minute dots on the periostracum (Fig. 4C). The flagellum is only about one quarter the length of the distal part of the distal part of the epiphallus and is distinctly hooked (Fig. 3C).

Animal: "Dark grey to black on dorsal surface, speckled with cream spots; more or less distinct, discontinuous thin creamy white line along the centre of the back; tentacles very dark; sole grey, with orange margins; mantle border orange." (D.F. McMichael, unpublished notes).

Distribution: (Fig. 6). New South Wales 29° 30'S 152° 00'E 33 miles east of Glen Innes (AM); 30° 00'S 152° 00'E Marengo (AM); 30° 00'S 152° 30'E Bellingen R. (QM), Dorrigo State Park (AM); 30° 00'S 153° 00'E Mt. Coryah (AM); 30° 30'S 151° 30'E New England National Park (N.P.) (AM); 30° 30'S 152° 00'E Melrose (AM), Styx R. (AM); 30° 30'S 152° 30'E Nambucca R. (QM); 31° 00'S 152° 00'E Mt. Boss (AM); 31° 00'S 152° 30'E Yessabah Cave (AM); 31° 30'S 151° 30'E Barrington Tops (AM); 31° 30'S 152° 00'E Wingham (AM); 32° 00'S 150° 30'E Scone (AM); 32° 00'S 151° 00'E Mt. Royal State Forest; 32° 00'S 151° 30'E Gloucester (AM), Upper Allyn R. (AM); 32° 00'S 152° 00'E Bulahdelah (AM), Myall Lake (AM), Wallis Lake (AM); 32° 00'S 152° 30'E Charlotte Head (AM); 32° 30'S 151° 00'E Bulga (AM); 32° 30'S 151° 30'E Ash Is. (AM); 32° 30'S 152° 00'E Port Stephens (AM).

Habitat: The species lives in rain-forest or wet sclerophyll forest.

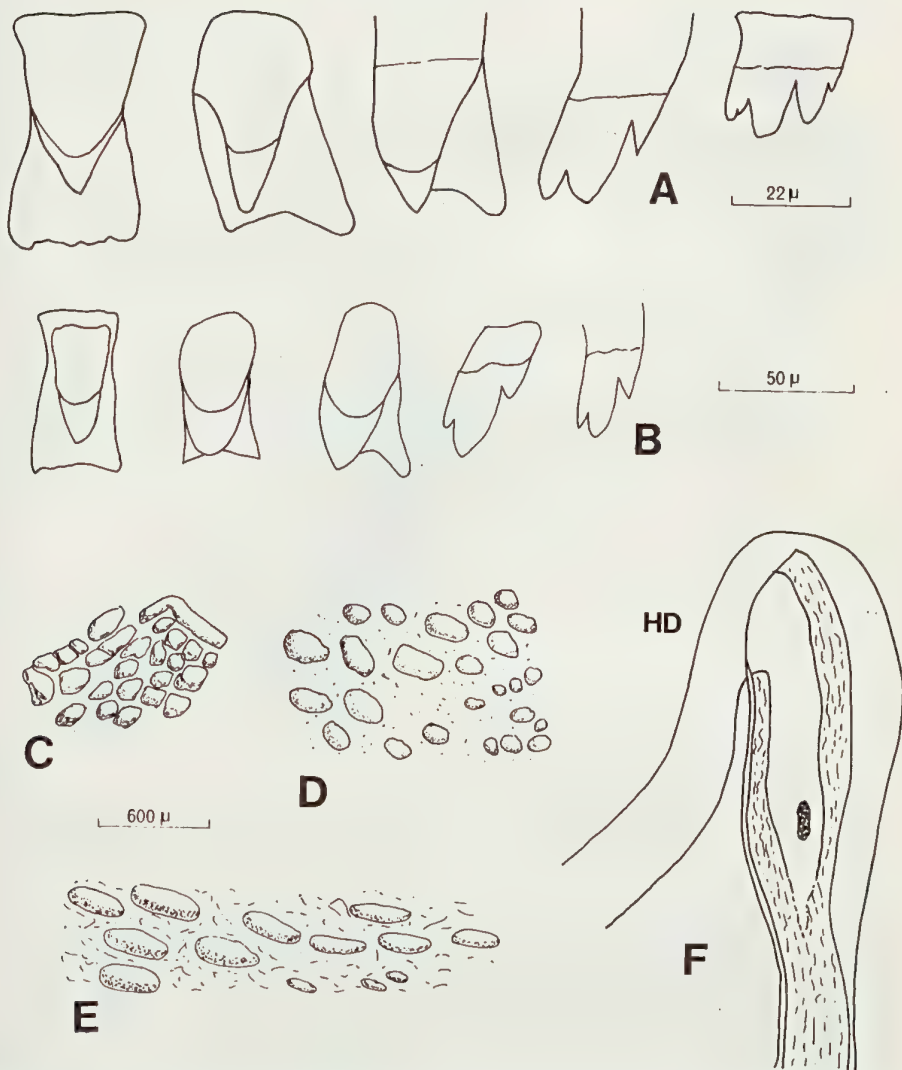


FIGURE 4. *Thersites richmondiana* (Reeve), Lamington National Park, Queensland. (QM). A-radula teeth, E-shell sculpture, F-carrefour region. *T. novaehollandiae* (Gray), New England N.P. (AM). B-radula teeth, D-shell sculpture. *T. mitchellae* (Cox), Tweed River (QM). C-shell sculpture. (HD hermaphrodite duct.)

THERSITES RICHMONDIANA (REEVE)

FIG. 1; 4A, E-F; 5; 14-16

Helix richmondiana Reeve 1852; pl. 70, sp. 365.

Type locality: Australia. Restricted to Richmond River by Pfeiffer (1853).

Location of type: not traced in the BM.

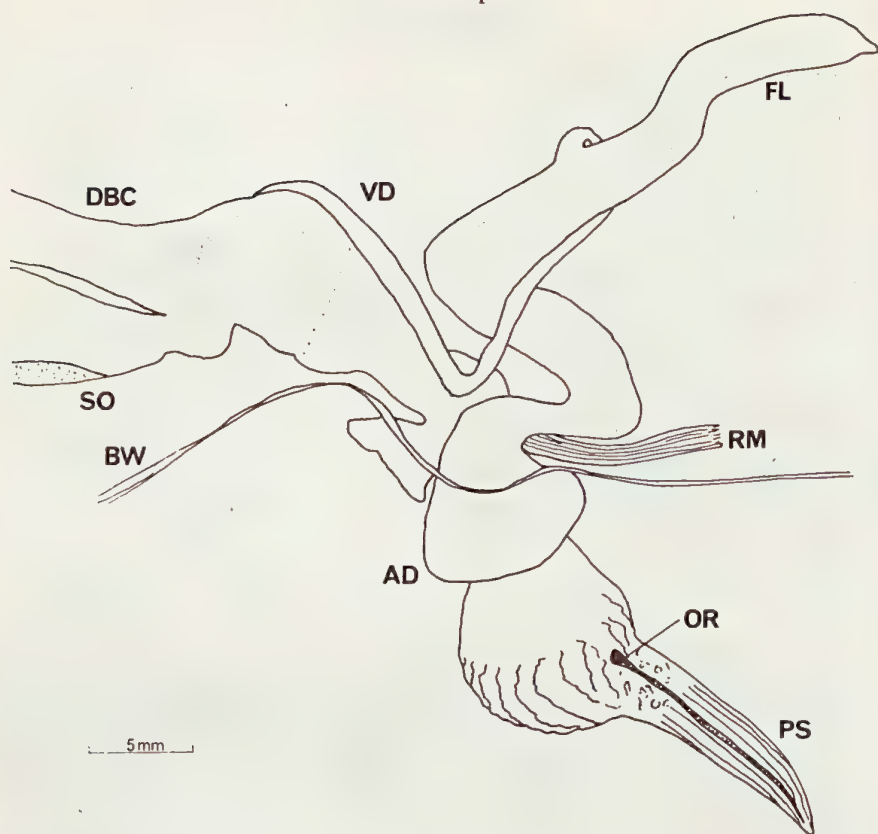


FIGURE 5. *Thersites richmondiana* (Reeve), Lamington National Park, Queensland. (QM). Extruded penis. (AD-atrial disc, BW-body wall, DBC-bursa duct, FL-flagellum, OR-orifice, PS-penial papilla, RM-retractor muscle, SO-spermoviduct, VD-vas deferens.)

Synonyms: *Annakelea tympanum* Iredale, 1937: 38, pl.3, Fig. 25. Type locality: Mt. Tambourine, South Queensland. Location of type: AM C100667. Iredale considered this "a giant relative of *novae-hollandiae*" but gave no reason for such an opinion.

Thersites darlingtoni Clench & Archer, 1938: 20, pl.1, Fig. 2. Type locality: MacPherson Range, Queensland National Park, 60 miles S. of Brisbane, Queensland. Location of type: Museum of Comparative Zoology, Harvard (MCZH) 99054. Clench and Archer stated "As compared with *T. richmondiana*, our species has a definitely less sharp keel." This is a variable feature as can be determined from examination of a large series of shells. Iredale (1938: 123) considered it a synonym of *A. tympanum*.

Diagnosis. The shell is large (30 mm high) and depressed (height:width 0.7:1) with an angulate periphery and often with a marked keel. Shell sculpture consists of scattered granules with fine periostracal wrinkles (Fig. 4E). Shell colour is often dark brown. The straight flagellum is about half the length of the distal part of the epiphallus.

Shell: The trochiform, acutely keeled shell of *T. richmondiana* has long aroused interest. Similarly keeled, though more depressed shells have been produced by *Caraculus* (Camaenidae, Greater

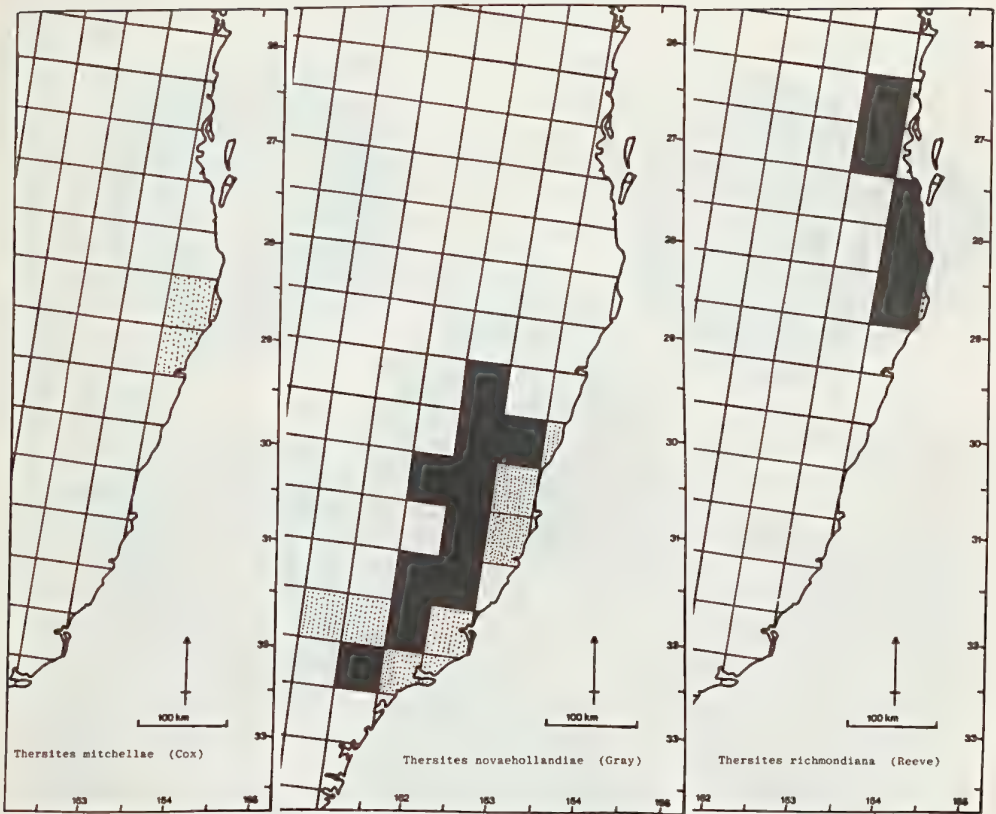


FIGURE 6. Distribution of *Thersites* according to half degree squares of latitude and longitude. Black — records based on dissected material, stipple — records based on shells only.

Antilles), *Pyrochilus* (Bradybaenidae, Moluccas) and *Ampelita* (Acavidae, Madagascar) and may be of adaptive value for a sub-arboreal way of life in tropical or sub-tropical forest.

The shell colour of *T. richmondiana* may be similar to that of the other two species of *Thersites*, and Pilsbry (1890: 91) called this forma *decolorata*. The usual form is dark brown, though there is an entirely albino shell from Nashaw in the Australian Museum.

Animal: The skin pigment is grey with yellow granules. The dorsal grooves on the neck are not deep but are clearly defined by a cream coloured band running between them from the ocular tentacles three quarters of the way back towards the collar.

Distribution: (Fig. 6). Queensland: 26° 30'S 152° 30'E Conondale (QM); 27° 00'S 152° 30'E Mt. Glorious (QM); 27° 30'S 153° 00'E Mt. Tamborine (QM); 28° 00'S 153° 00'E Lamington N.P. (QM), Natural Bridge N.P. (QM), Warrie N.P. (QM); New South Wales 28° 00'S 153° 00'E Mt. Warning (QM); 28° 30'S 153° 00'E Booyong (AM), Dunoos (AM), Nashaw (AM), Whian Whian (AM); 28° 30'S 153° 30'E Mullumbimby (AM), Wollongbar (AM).

Habitat: Rain-forest or wet sclerophyll forest up to 900 m. The animal lives under the bark of trees or under logs on the ground and is entirely nocturnal. It will sometimes feed on leaf litter on the ground but is usually found on the lower parts of trees (up to 5 m) feeding on fungi.

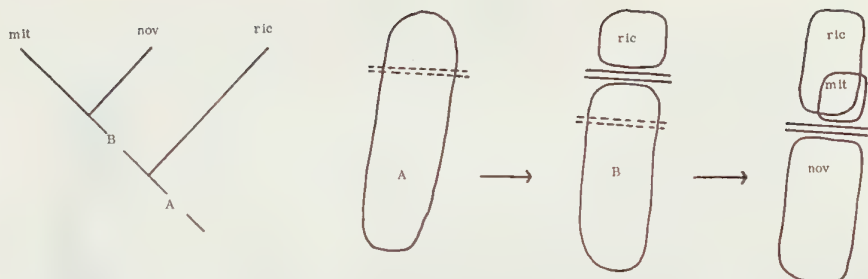


FIGURE 7. An hypothesis of speciation of *Thersites*, mt = *T. mitchellae* (Cox), nov = *T. novaehollandiae* (Gray), ric = *T. richmondiana* (Reeve).

SHELL SIZE AND SHAPE

Sufficient specimens of only one population of each of the three species of *Thersites* were available for statistical study. Measurements of shell height and width were made on mature unbroken shells and recorded in millimetres. The homogeneity of the sample of *T. mitchellae* is suspect as it consisted of shells in the Australian Museum labelled "Byron Bay" which may have come from a number of separate populations. The shells of *T. novaehollandiae* were collected by S.W. Jackson at Billey's Scrub, Dorrigo in 1900 and the shells of *T. richmondiana* by the author at Binna Burra, Lamington N.P. in 1976 and both represent samples from single biological populations.

Mean values for shell size are presented in Table 1, and the difference between mean height or width of each sample is highly significant (Student's *t*, one sided test, $P < 0.01$). Shell height constituted the better characterisation of each sample with no overlap in the range of values. These measurements cannot be taken as characteristic of each species and further populations must be studied. A small shell of *T. novaehollandiae* from Mt. Kaputar was only 14.6 mm high and 24.8 mm wide and could not have been drawn from the Dorrigo population ($P < 0.01$). A large shell in the Australian Museum labelled "Dorrigo" measured 28.7 mm high and 40.5 mm wide and could not have been drawn from the Billey's Ck. population ($P < 0.005$) but agrees with the Lamington population of *T. richmondiana* ($P > 0.15$). Care is clearly necessary in using size alone as a specific criterion within the genus.

The way in which height and width vary together gives a measure of the shape of the shells of *Thersites*. The ratio of mean height to mean width of the sample of *T. mitchellae* (0.94) seems distinct from the values for the other two samples but no precise meaning can be given to these figures as height and width are not independent. Highly significant linear regression lines relate height and width (Table 2). As the regression of width on height approaches that of height on width the coefficient b_{WH} approaches $1/b_{HW}$. Only in the case of *T. richmondiana* are these values reasonably close. Comparison of the values of b_{WH} for the three samples showed that the differences were not significant (Student's *t*, one sided test, $P > 0.15$). The large covariances of height and width in samples of *Thersites* mean that shell shape is not a very reliable criterion for species recognition.

FIGURES 8-16

8-10 *Thersites mitchellae* (Cox). Broken Head, Byron Bay, New South Wales. AM C105563 Jackson leg.

11-13 *T. novaehollandiae* (Gray). Marengo State Forest, Dorrigo, New South Wales. AM C102866 Greer leg.

14-16 *T. richmondiana* (Reeve). Wollongbar, Richmond River district, New South Wales. AM C105562 Helms leg.

All natural size.

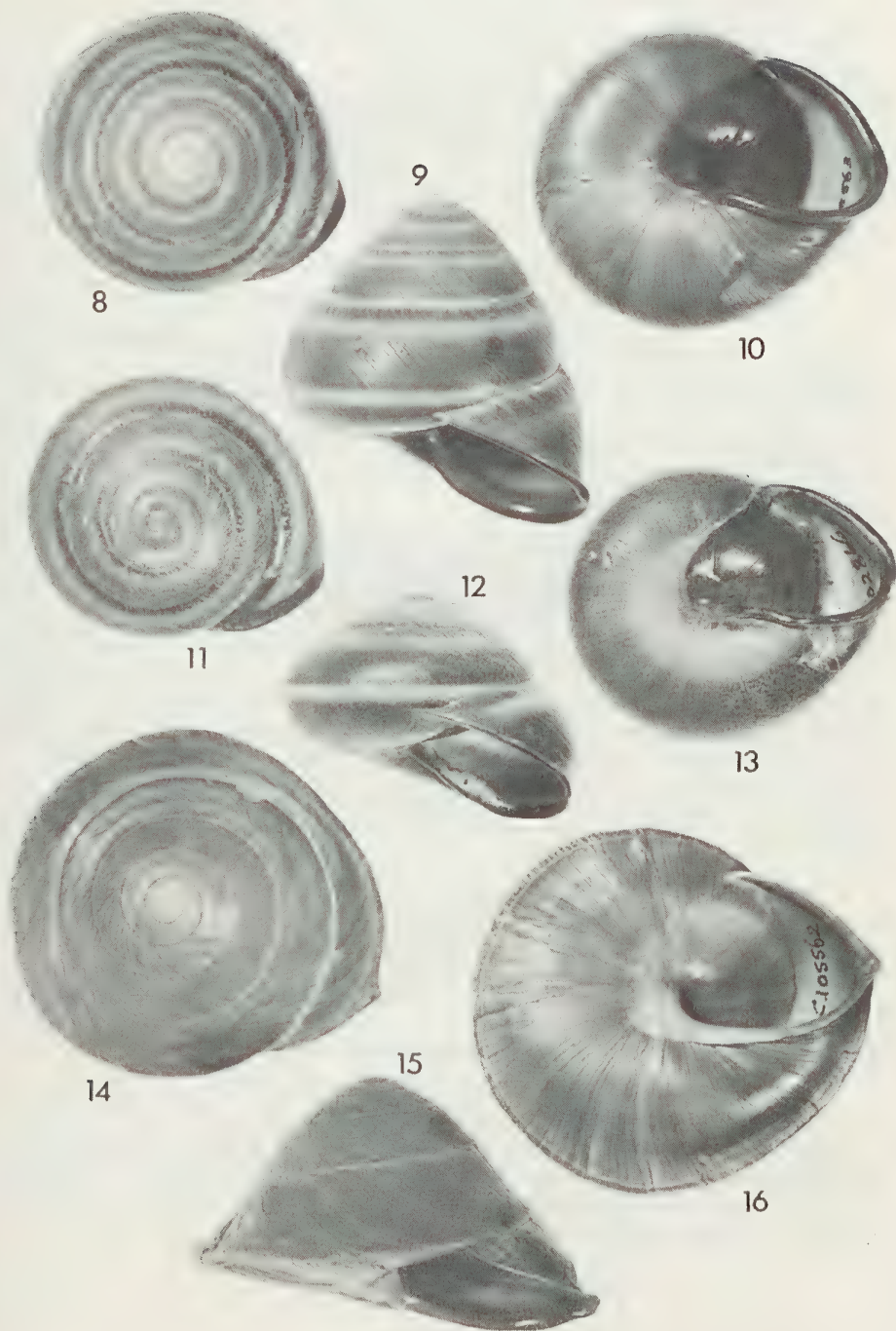


Table 1. Estimates of size (mm) of the shell of *Thersites*, 16 specimens in each sample.

	Height			Width		
	Mean	Standard error	Range	Mean	Standard error	Range
<i>T. mitchellae</i> Byron Bay (AM)	40.6	0.89	35.5 - 44.8	42.8	0.83	39.5 - 46.6
<i>T. novaehollandiae</i> Dorrigo (AM)	21.0	0.55	17.1 - 25.0	33.8	0.50	30.9 - 38.7
<i>T. richmondiana</i> Lamington (QM)	31.7	0.42	28.9 - 34.7	45.2	0.54	41.3 - 47.8

Table 2. Estimates of shape of *Thersites* in terms of height (H) and width (W)

	Ratio mean H:W	Correlation H with W	Regression coefficients				Significance of regression	
			a_W	a_H	b_{WH}	$1/b_{HW}$	F	P
<i>T. mitchellae</i> Byron Bay (AM)	0.94	0.63	18.8	11.7	0.59	1.69	9.3	0.009
<i>T. novaehollandiae</i> Dorrigo (AM)	0.62	0.75	19.4	-6.7	0.68	1.45	15.7	0.001
<i>T. richmondiana</i> Lamington (QM)	0.70	0.73	15.4	6.3	0.94	1.06	18.0	0.001

SPECIATION OF *THERSITES*

If we assume that evolutionary trends within the genus have been in the direction of producing a more depressed, keeled shell and for shortening of the relative length of the flagellum, then *T. mitchellae* has diverged least from a common antecedent (Fig. 7, A). An early vicariant event was the separation of *T. richmondiana* from antecedents to *T. mitchellae* and *T. novaehollandiae* (B). Selection by predation could have led to the predominance of the dark morph of *T. richmondiana*. A second event was the separation of *T. novaehollandiae* to the south and *T. mitchellae* to the north of the Clarence River. This hypothesis implies that the production of depressed shells occurred on two separate occasions, which is insufficiently supported by the morphological evidence. It is favoured because it seems more in accord with the present distribution of the species. A serological study might clarify the situation. Barriers responsible for these events are no longer in evidence and it will be of future interest to discover if such patterns are exhibited by other groups.

RELATIONSHIPS TO OTHER GENERA

Until the details of the anatomy of other camaenid genera, both in eastern Australia and in New Guinea, are made known, it is rather unprofitable to speculate about the relationships of the genus. *Thersites* possesses a number of features which are possibly unique derivations within the taxa of interest: the particular kind of granular sculpture, the dorsal coloured line on the neck, the bend in the bursa duct and the large imperforate conical papilla in the penis. Certainly these features are not possessed by *Hadra*, *Sphaerospira*, or *Meridolum* which seem more closely related to each other than they do to *Thersites*.

ACKNOWLEDGEMENTS

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A NEW RECORD OF *THECACERA PENNIGERA* (MONTAGU, 1815)
(OPISTHOBRANCHIA: POLYCERIDAE) FROM NEW SOUTH WALES

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Joyce Allan (1957:4) reported some details of specimens of the then western European species *Thecacera pennigera* (Montagu, 1815) found in July 1951 during sea-water conduit inspections at White Bay Power Station in the upper reaches of Sydney Harbour, New South Wales. The species has not been reported again from Australia, but has been described from Brazil (Marcus, 1957), Japan (Baba, 1960), and New Zealand (Willan, 1976). In an excellent paper, Willan (1976) reviewed what is known of *T. pennigera*, and synonymized with it *T. maculata* Eliot from Pakistan and *T. lamellata* Barnard from South Africa. The species thus has a circumglobal distribution, except that it is not reported from the Pacific coast of North and South America or the Atlantic coast of North America.

In July 1970, another specimen of *T. pennigera* was collected and photographed in Port Hacking, south of Sydney Harbour, indicating the continued presence of the species in eastern Australian waters. Data for this specimen is:

Ship Rock, Port Hacking, New South Wales, 5 m among sponges, ascidians, etc, July 1970, coll. Neville Coleman, 1 specimen live length 15 mm (F30107). Alive, the specimen matched precisely the description and figures of New Zealand specimens (Willan, 1976), even to the details of postbranchial processes with white shining granules at the tip, below which a golden zone and then the translucent base. In the preserved specimen, a deep pit is present on each side of the head below the base of each rhinophoral sheath.

The deep pit on each side of the head in *T. pennigera*, and also in *T. picta* Baba (1972), has been commented upon by Willan (1976). In the large southern Australian polycerid *Tambja verconis* (Basedow & Hedley), similar deep pits are present dorsally to the oral tentacles, and have a sensory purpose in short distance location of live *Bugula* and orientation of the head and mouth prior to feeding.

It is of interest to note that the Australian distribution of *T. pennigera*, Sydney Harbour to Port Hacking, falls within that of another apparent introduction *Polycera capensis* (Quoy & Gaimard), originally from South Africa. First noted in Sydney Harbour in 1927 (Allan, 1931), *P. capensis* ranges from Broken Bay (28 km N.) to Kiama (100 km S.), all collections other than those from Sydney Harbour post-dating 1947.

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A NEW SPECIES OF *BURSA* FROM DEEP WATER OFF THE PHILIPPINE ISLANDS

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SUMMARY

Bursa (*Bufonariella*) *rehderi* n. sp. is described from deep water around the Philippine Islands. Watson's (1886) Philippines specimen identified as *Ranella fijiensis* is probably a specimen of *B. rehderi*; both it and the holotype of *R. fijiensis* are figured.

INTRODUCTION

Among several rare gastropods of the family Bursidae lent to the writer by the United States National Museum are several lots of an unusual thin-shelled species of *Bursa* collected at 20 stations around the Philippine Islands, in 210 to 640 m, by the United States Bureau of Fisheries Steamer "Albatross". The opportunity is taken to name the new species in honour of Dr Harald Rehder, Zoologist Emeritus, United States National Museum, in the year of his retirement from a long career of valuable contributions to molluscan taxonomy.

TAXONOMY

Class Gastropoda

Family Bursidae

Genus *Bursa* Röding, 1798

1798. *Bursa* Röding, Museum Boltenianum (2): 128. Type species (by subsequent designation, Oyama, 1964): *Bursa monitata* Röding, 1798 (= *Murex bufonius* Gmelin 1791), Recent, Indo-West Pacific.

1899. *Pseudobursa* Rovereto, Atti Soc. Ligust. Sci. Nat. Geog., 10:6. Unnecessary replacement for *Bursa* Röding, 1798.

The first type designation for *Bursa* to select a species expressly included by Röding (1798: 128) is that by Oyama (1964: 33) who cited: "Type-species (s.d., Jousseaume, 1881): *Murex bufonius* Gmelin [in *Bursa monitata* Röding]", and thereby designated *Bursa monitata* Röding as type species of *Bursa* (International Code of Zoological Nomenclature, Article 69 (a) iv).

Subgenus *Bufonariella* Thiele, 1929.

1929. *Bufonariella* Thiele, Handbuch der Systematischen Weichtierkunde, 1 (1): 284. Type species (by monotypy): *Murex scrobilator* Linnaeus, 1758, Pliocene to Recent, Mediterranean.

Bufonariella is here used as a subgenus of *Bursa* distinguished by its thinner and more finely sculptured shell, its shorter posterior apertural canal, its lower and narrower varices, and its taller

spire than those of *Bursa* (*sensu stricto*). The operculum has its nucleus at the abaxial edge of the anterior end and the varices of most species are aligned up the sides of the spire, at least on early whorls, and these features show that *Bufonariella* is closely related to *Bursa*.

Bursa (*Bufonariella*) *rehderi* n. sp.

Figs. 1-8

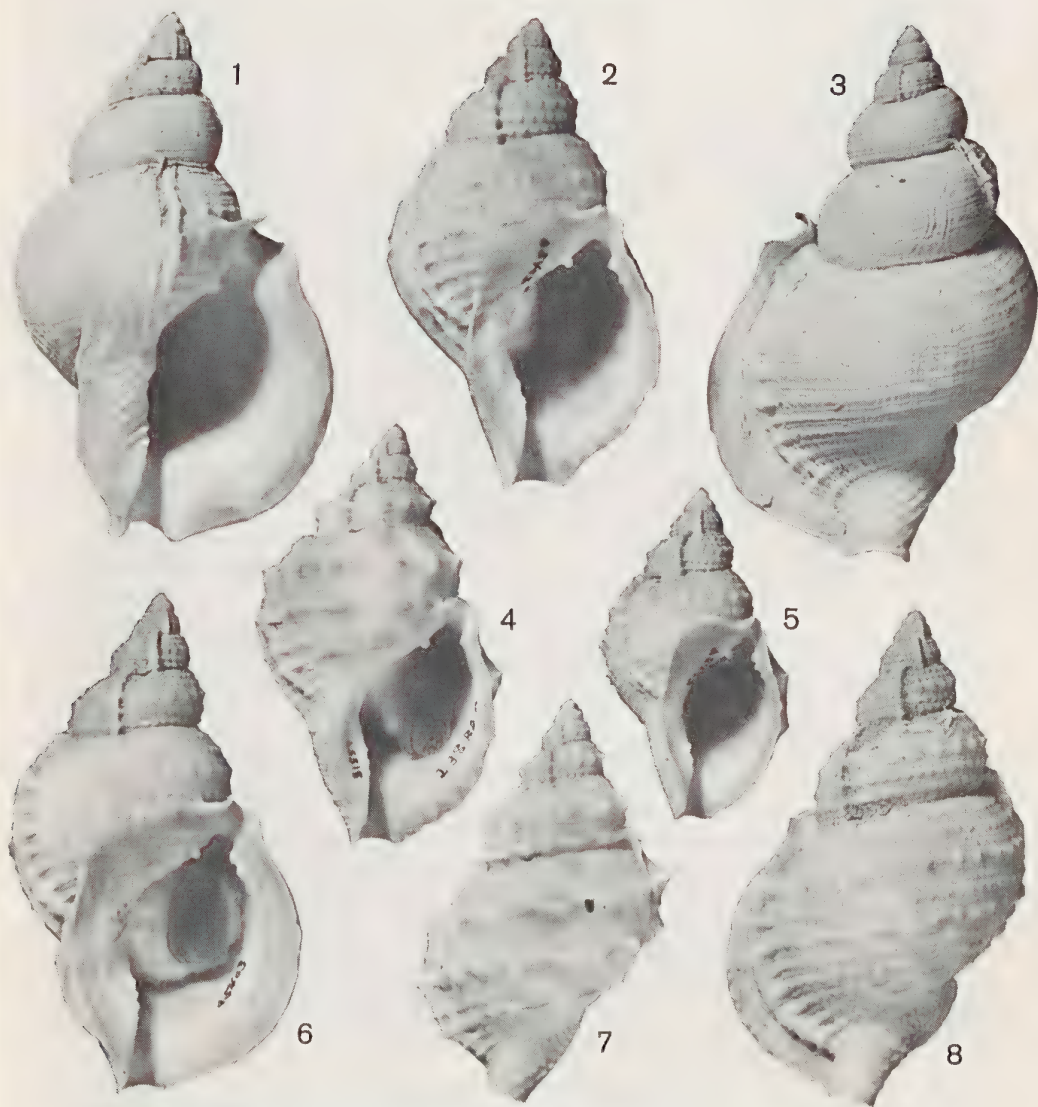
Shell of moderate size, wide for the subgenus, light and thin, finely sculptured, with strongly rounded whorls and a large aperture. Varices small, thin and relatively high, aligned up spire sides (or nearly so) on first three or four whorls but becoming progressively more widely spaced over last one to two whorls so that they are spaced as in *Tutufa* and *Cymatiidae* over the last whorl of large shells; weakly hollowed, and thus weakly buttressed by spiral cords, on abapertural edge; succeeded on adapertural edge by thin, high, flared, former outer lips that become progressively more expanded down the shell. Sculpture of initial few teleoconch whorls consists of four or five spiral rows of small, slightly pointed, closely spaced nodules, 10 to 15 in each intervariceal space in each row; nodules of peripheral row slightly larger than others. On some specimens, nodules remain of similar size to those of initial whorls down entire shell; on other specimens nodules increase in size progressively down the shell, so last whorl bears only three rows of five or six large, pointed, anteroposteriorly compressed nodules in each intervariceal space; and on other specimens, nodules decrease in size progressively down the shell so last few whorls are almost smooth, bearing scarcely raised, narrow, spiral cords only. Specimens with prominent nodular sculpture on last few whorls bear nodules on varices where they are crossed by spiral cords, whereas varices of weakly sculptured specimens have a smoothly curved outline. Entire shell surface crossed by regular, low, fine, closely spaced, spiral lirae, crossed by even finer and more closely spaced incremental lirae. Aperture unusually large for *Bufonariella*, with short, widely open anterior and posterior siphonal canals; inner and outer lips both almost smooth, expanded into thin, flared flanges covering parietal area, columella and varix, degree of expansion increasing markedly with shell size so lips are most widely flared in largest specimens; one small, narrow parietal ridge and three or four low, narrow columellar ridges on inner lip; many weak, low folds around internal edge of outermost flare of outer lip in small specimens, reduced to one or two weak folds at top and bottom of otherwise smooth lip on most large shells (about 16 weak folds on holotype are arranged in irregular pairs). Aperture white; exterior cream to pale reddish brown, pattern arranged in faint axial flames on some specimens, and as slightly darker reddish brown streaks on spiral cords between white nodules on many specimens; largest specimen black and fawnish grey (presumably stained). Protoconch typical of *Bursidae*, relatively large, equidimensional-turbinate, of three rounded whorls; surface details eroded from all available specimens. Operculum thin, medium brown, subrectangular, with nucleus at anterior abaxial corner.

Dimensions: height 70.3 mm, diameter 40.2 mm (holotype); height 73.5 mm, diameter 44.0 mm (largest paratype, USNM 205474); height 65.0 mm, diameter 36.4 mm (paratype, USNM 240450); height 59.2 mm, diameter 34.1 mm (widest paratype, coarse sculpture, USNM 238820); height 45.0 mm, diameter 26.0 mm (smallest paratype, USNM 240450).

Holotype (USNM 240450), 6 paratypes (lots 238820, 230654, 240450, 205474) and 16 other lots of specimens in United States National Museum; one paratype (WM 12070) presented to New Zealand Geological Survey.

Localities: Holotype and three paratypes, U.S. Bureau of Fisheries (USBF) Station 5403, 333 m (182 fm), on green mud, off Abgao, Leyte, Philippine Islands (USNM 240450, WM 12070). Other paratypes: USBF Sta. 5518, 365 m (200 fm), off Pt. Tagolo, Mindanao, Philippines (three, USNM 238820); USBF Sta. 5191, 490 m (268 fm), Tañon Strait, Philippines (one, USNM 230654); USBF Sta. 5188, 9° 44'N, 123° 14' 20"E, Tañon Strait due west of Alegria, Cebu I., and midway between coasts of Cebu and Negros Islands, Philippines, 547 m (299 fm) (largest paratype, USNM 205474).

Other specimens, not seen (not designated paratypes): USBF Sta. 5508, off Iligan, Mindanao, Philippines, 494 m (270 fm) (one, USNM 238695); USBF Sta. 5506, off Tacnipa, Mindanao, Philippines, 479 m (262 fm) (one, USNM 238679); USBF Sta. 5403, off Capitancillo I., N. Cebu, Philippines, 333 m (182 fm) (three, USNM 287820); USBF Sta. 5216, off Claveria, Burias, Philippines, 393 m (215 fm) (one, USNM 280554); USBF Sta. 5118, Balayan Bay, Luzon, Philippines, 353 m (193 fm) (one, USNM 235381); USBF Sta. 5280, off Malvatuan I., W. Luzon, Philippines, 353 m (193 fm) (one, USNM 237548); USBF Sta. 5189, Tañon Strait, Philippines, 549 m (300 fm) (four, USNM 229275); USBF Sta. 5398, off Gigantangan I., N.W. Leyte, Philippines, 208 m



FIGURES 1-8. *Bursa (Bufonariella) rehderi* n. sp., Philippine Islands; all specimens in U.S. National Museum (all natural size).

1, 3. largest paratype, U.S. Bureau of Fisheries (USBF) Sta. 5188, Tañon Strait due west of Alegria, Cebu I., 547 m (USNM 205474), whitened with ammonium chloride.

2, 5. paratypes, USBF Sta. 5403, off Abgao, Leyte, 333 m (USNM 240450).

4, 7. paratypes with prominent sculpture, USBF Sta. 5518, off Pt Tagolo, Mindanao, 365 m (USNM 238820).

6, 8. holotype, USBF Sta. 5403, off Abgao, Leyte, 333 m (USNM 240450).

(114 fm) (two, USNM 287613); USBF Sta. 5404, S of Dupon Bay, Leyte, Philippines, 347 m (190 fm) (two, USNM 229370); USBF Sta. 5407, off Dupon Bay, Leyte, Philippines, 640 m (350 fm) (two, USNM 238269); USBF Sta. 5519, off Pt Tagelo, N. Mindanao, Philippines, 333 m (182 fm) (four, USNM 238840); USBF Sta. 5402, off Villalia, Leyte, Philippines, 344 m (188 fm) (21, USNM 238242); USBF Sta. 5535, SE of Pt. Tañon, Cebu, Philippines, 567 m (310 fm) (two, USNM 238896); USBF Sta. 5409, W. of Pacijan I., W. of Cebu, Philippines, 346 m (189 fm) (one, USNM 238292); USBF Sta. 5405, off Dupon Bay, Leyte, Philippines, 479 m (262 fm) (12, USNM 238256); USBF Sta. 5406, off Ponson I., Camotes Islands, Philippines, 545 m (298 fm) (six, USNM 288045).

Bursa (Bufonariella) rehderi differs strongly from all previously named species of the subgenus in its relatively wide shape, its strongly inflated whorls, its thin shell, its large aperture, and its prominently flared inner and outer apertural lips. The large range of variation in shape, apertural features, and size of sculptural nodules in a small geographic area is seen also in other, more typical species of *Bursa (Bufonariella)* such as the Mediterranean *B. scrobilator* (Linnaeus), the widespread Indo-West Pacific and Caribbean *B. granularis* (Röding), and especially the Panamic *B. caelata* (Broderip). The spire is taller and the shell is thinner and more finely sculptured in *B. rehderi* than in species of *Bursa* (sensu stricto), and these features leave little doubt that it belongs in *Bursa (Bufonariella)*, but examination of the radula will be necessary to confirm its position.

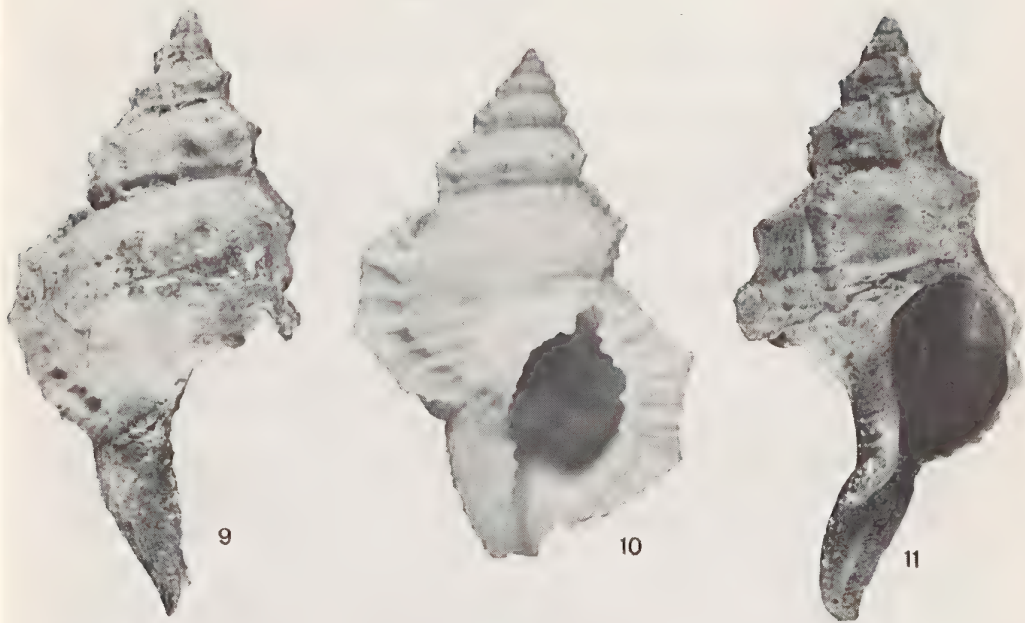
The relatively low spire and wide, slightly dorsoventrally compressed shape of *Bursa (Bufonariella) rehderi* lend it a superficial resemblance to species of *Bufonaria* Schumacher, the genus of Bursidae most commonly encountered on tropical continental shelves and in deeper water. However, the operculum of *Bufonaria* has its nucleus in the centre of the adaxial margin, so resembling operculae of *Phalium* and related Cassidae, and clearly differing from the abapical opercular nucleus of *B. rehderi* and other species of *Bursa* (sensu lato). Also *B. rehderi* lacks the strictly aligned, laterally expanded varices and more strongly dorsoventrally compressed shell of species of *Bufonaria*.

When he described *Ranella fijiensis*, Watson (1881: 270) included only one specimen, from "Challenger" sta. 173, lat. 19°09'35"S, long. 170°41'50"E, off Fiji, in 315 fm (576 m), on coral mud (in British Museum (Natural History), No. 1887.2.9.1217). Later (Watson 1886: 397) he included a second specimen, from "Challenger" sta. 204A, lat. 12°04'3"N, long. 122°09'E, off the Philippine Islands, 100 to 115 fm (183-210 m), on green mud (in British Museum (Natural History), No. 1887.2.9.1218).

The holotype of *Ranella fijiensis* (Fig. 10) was compared by Watson with both *Bufonaria nobilis* (Reeve) and *Bursa (Bufonariella) affinis* (Broderip) (= *B. granularis* Röding) but is clearly a species of *Bursa (Bufonariella)* related to *B. granularis*. It resembles *B. granularis* and differs from *B. rehderi* n. sp. in its finely granulate surface sculpture and relatively wide, prominent varices that are aligned up the spire sides, and differs from *B. granularis* in its shorter spire, more angled whorls, and even wider varices. However, the Philippines specimen identified by Watson as *Ranella fijiensis* (Fig. 9, 11) is not conspecific with the holotype, and its long columella, widely reflected inner lip callus, almost smooth surface between relatively large widely spaced nodules, and relatively widely separated varices (ca. 200° apart) strongly suggest that it is a broken, worn, encrusted specimen of *Bursa (Bufonariella) rehderi* n. sp. The specimen is 75.1 mm high (slightly larger than the largest paratype of *B. rehderi*), whereas the holotype of *B. fijiensis* is 53.6 mm high and 35.0 in diameter. If correctly assigned to *B. rehderi*, this is the only specimen known to the writer in collections other than the U.S. National Museum and the New Zealand Geological Survey.

ACKNOWLEDGEMENTS

I wish to thank Dr Harald A Rehder, U.S. National Museum, for much help including the loaning of specimens and the provision of locality data; Mollusca Section, British Museum (Natural History), for photographs 9 to 11; and Drs P.A. Maxwell and C.A. Fleming, N.Z. Geological Survey, for comments on the manuscript. Photographs 1 to 8 are by D.L. Homer, N.Z. Geological Survey.



FIGURES 9-11.

- 9, 11. *Bursa (Bufonariella) rehderi* n. sp., specimen identified by Watson (1886) as *Ranella fijiensis* Watson, 1881; "Challenger" sta. 204A, off Philippine Islands, 100-115 fm (183-210 m); British Museum (Natural History) No. 1887.2.9.1218; enlarged X 1.1.
10. *Bursa (Bufonariella) fijiensis* (Watson, 1881), holotype of *Ranella fijiensis* Watson, "Challenger" sta. 173, off Fiji, 315 fm (576 m); British Museum (Natural History) No. 1887.2.9.1217; enlarged X 1.4.

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MARIANINA ROSEA (PRUVOT-FOL, 1930) (OPISTHOBRANCHIA :
DENDRONOTACEA): FURTHER RECORDS FROM AUSTRALIA

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Since reporting *Marianina rosea* (Pruvot-Fol, 1930) from 'The Blows', Point Quobba, Western Australia (Burn, 1974: 305), additional material of this pretty little dendronotacean has been received from three widely separated localities. The specimens have been deposited in the National Museum of Victoria.

Duncombe Bay, Norfolk Island, 14 m in cavern, 25 September 1976, coll. J.E. Watson, 1 specimen preserved length 7 mm (F30099). In life, body deep mauve, tentacles, velar and lateral processes, lobe of rhinophoral sheaths and stripe on tail shining cream, rhinophores bright red.
New record for Norfolk Island.

North Solitary Island, Coffs Harbour, New South Wales, 20 m under rock, 26 September 1976, coll. Neville Coleman, 1 specimen preserved length 5 mm (F30101). In life, body mauve, tentacles, velar and lateral processes, lobe of rhinophoral sheaths and stripe on tail yellowish-cream, rhinophores orange red.
New record for New South Wales.

Knob Point, Stokes Bay, South Australia, 10 m on blue ascidian, 6 March 1978, coll. Neville Coleman, 1 specimen preserved length 4 mm (F30100). In life, body bright bluish-mauve, tentacles, velar and lateral processes deep red, stripe on tail a reddish tinge, rhinophores lighter red. The velar and lateral processes are short and small in this specimen, and the rhinophoral sheaths have no lobe. There are three pairs of lateral processes.
New record for South Australia.

Further distribution: Île des Pins, New Caledonia (Pruvot-Fol, 1930); Aranuka, Gilbert Islands (Odhner, 1936); Guam, Anatahan and Pagan Islands, Marianas (Carlson & Hoff, 1973); Point Quobba, Western Australia (Burn, 1974).

With the exception of the South Australian specimen, all references to living *M.rosea* indicate little variation in body shape and colouration. The South Australian specimen differs from the typical form in lacking a lobe on the rim of the rhinophoral sheaths, in having short and small velar and lateral processes, and in the red colouration of the tentacles, velar and lateral processes. Further material may show this to be an isolated population worthy of subspecific separation, or perhaps another species.

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PRUVOT-FOL, A., 1930. Diagnoses provisoires (incomplètes) des espèces nouvelles et liste provisoire des mollusques nudibranches recueillis par Mme A. Pruvot-Fol en Nouvelle-Calédonie (Île des Pins). *Bull. Mus. Nation. Hist. Nat.* (2), 2(2): 229-232.

NOTE ADDED IN PROOF

A second specimen from the above-mentioned South Australian locality has the same basic colouration and characteristics, except that the tentacles are cream, the upper part of the rhinophoral sheaths is tinted rose-red and the rim bears a long pointed lobe of the same colour, and the velar and lateral processes are rose-red.

Knob Point, Stokes Bay, N coast of Kangaroo Island, South Australia, c.15m in rocks and gutters, 5 March 1978, coll. A. & R. Kuiter, 1 specimen (Australian Museum C109319).

NEW RECORDS AND SPECIES OF CYMATIIDAE
(GASTROPODA : PROSOBRANCHIA) FROM
THE KERMADEC ISLANDS, NORFOLK RIDGE AND NEW ZEALAND

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SUMMARY

A new subgenus and species, *Distorsio* (*Distorsionella*) *lewisi*, are proposed for a small, weakly distorted shell combining the reticulate protoconch of *Sassia* (*Sassia*) with a long, weakly armed aperture and the operculum, proboscis, radula, and ridged columellar base of *Distorsio*; specimens are from the Kermadec Islands, Reinga Ridge and Norfolk Ridge. *Sassia* (*Sassia*) *marshalli* n. sp. is described from the Kermadec Islands. New records are *Distorsio constricta habei* Lewis from the Kermadec Islands (previous records from southern Japan, but recorded here also from the Philippines and north-western Australia), *Sassia* (*Sassia*) *nassariformis remensa* (Iredale) from the Bay of Plenty, New Zealand, *Sassia* (*Proxicharonia*) *palmeri* (Powell) from the Kermadec Islands and Norfolk Ridge, and *Ranella olearium* (Linnaeus), *Fusitriton magellanicus laudandus* Finlay, and *Cymatona kampyla kampyla* (Watson) from the Kermadec Islands.

INTRODUCTION

The subtidal molluscan fauna of the ridges and seamounts north of New Zealand and east of Australia is only slowly being revealed, as successive oceanographic expeditions dredge and trawl more successfully from the area. At present the situation is about that reached around New Zealand two decades ago, so it is not surprising that the following new records from the Kermadec Ridge have been brought to light by the New Zealand Oceanographic Institute and by Mr Alex Black on R.V. "Acheron" (material in N.Z. National Museum, Wellington). The seven species recorded here from the Kermadec Islands include (1) *Sassia* (*Proxicharonia*) *palmeri*, only recently recognised around northern New Zealand, and now seen to be a member of the restricted southwest Pacific fauna (including also *Neothais smithi*, *Semicassis royanum*, *Casmaria ponderosa perryi*, *Bursa* (*Lampadopsis*) *verrucosa*, and others). (2) a subspecies of *Distorsio* previously recorded only from southern Japan but a member of a species occurring also in the Caribbean and Panamic western America. (3) a distinctive new Kermadec Islands species of the formerly cosmopolitan but now sparsely distributed genus *Sassia* (sensu stricto).

(4) a new species of a new subgenus *Distorsio* (*Distorsionella*), apparently endemic to the area. (5) the widely distributed *Ranella olearium* (Linnaeus). (6 & 7) the widespread New Zealand and south eastern Australian taxa *Fusitriton magellanicus* and *Cymatona kampyla*. The opportunity is taken to record the eastern Australian taxon *Sassia* (*Sassia*) *nassariformis remensa* (Iredale) from New Zealand.

Other Cymatiidae in New Zealand Oceanographic Institute and National Museum dredged samples from the Kermadec Islands include *Charonia lampas rubicunda* (Perry), *Ranella australasia australasia* (Perry), and *Septa parthenopea* (von Salis Marschlin), all recorded previously on beaches at the Kermadec Islands (Iredale 1910; Oliver 1915). The following 18 taxa of Cymatiidae are now known from the Kermadec Islands:

Subfamily Ranellinae

- Cabestana* (*Cabestana*) *spengleri* (Perry, 1811)
- tabulata tabulata* (Menke, 1843)
- Cabestana* (*Turritriton*) *labiosa* (Wood, 1828)
- Charonia lampas rubicunda* (Perry, 1811)
- Cymatona kampyla kampyla* (Watson, 1885)
- Fusitriton magellanicus laudandus* Finlay, 1927
- Ranella australasia australasia* (Perry, 1811)
- olearium* (Linnaeus, 1758)
- Sassia* (*Sassia*) *marshalli* n. sp.
- Sassia* (*Austrosassia*) *parkinsonia* (Perry, 1811)
- Sassia* (*Proxicharonia*) *palmeri* (Powell, 1967)

Subfamily Cymatiinae

- Ranularia caudata* (Gmelin, 1791)
- dunkeri iredalei* Beu, 1968
- Septa exarata exarata* (Reeve, 1844)
- parthenopea parthenopea* (von Salis Marschlin, 1793)
- vespacea* (Lamarck, 1816)

Subfamily Distorsioninae

- Distorsio* (*Distorsio*) *constricta habei* Lewis, 1972
- Distorsio* (*Distorsionella*) *lewisi* n. sp.

TAXONOMY

Family Cymatiidae

Subfamily Ranellinae

Genus *Sassia* Bellardi, 1873

Subgenus *Sassia* sensu stricto

Sassia Bellardi, 1873: 219. Type species (by subsequent designation, Cossmann, 1903): *Triton apenninicum* Sassi, 1827, Miocene and Pliocene, Europe.

Phanozesta Iredale, 1936: 309. Type species (by original designation): *Phanozesta remensa* Iredale, 1936, Recent, New South Wales.

The writer (Beu 1976: 305) has given reasons for regarding *Austrotriton* Cossmann, 1903 and *Austrosassia* Finlay, 1931 as subgenera of *Sassia* Bellardi, 1873. Diagnostic features of *Sassia* (*Sassia*) are the cancellate, turbiniform protoconch of 2½-3 whorls, the small size, the elongate form with tall spire, the small muriciform aperture with flared lips, and the six or seven prominent denticles inside the outer lip.

Recent taxa previously referred to *Sassia* (*Sassia*) are the three geographic subspecies *S. nassariformis nassariformis* (Sowerby, 1902), South Africa, *S. nassariformis remensa* (Iredale, 1936) (Figs. 6, 13, 15, 16), New South Wales and newly recorded below from north-eastern New Zealand, and *S. nassariformis semitorta* (Kuroda & Habe in Habe, 1961) (Figs. 12, 14), Japan, and the

Japanese species *S. sakuraii* (Habe, 1961). All four are extremely similar in general appearance and coloration, in their narrow shape, in their strongly abaperturally hollowed varices, and in their sculpture of several rows of evenly spaced, small, narrowly rounded nodules at the junctions of equally prominent spiral cords and collabral costae. The new species named below differs from other Recent taxa in lacking prominent spiral cords, but agrees with them in all other diagnostic features.

The type species of *Sassia*, the European Miocene and Pliocene *S. apenninica* (Sassi) (Figs. 17, 18), differs from Recent taxa listed above only in its slightly shorter spire, slightly more prominent varices, and more widely spaced rows of nodules of which the peripheral two rows are more prominent and more sharply antero-posteriorly compressed than those of Recent taxa. Whatever the generic position of the many poorly known European fossil species currently placed in *Sassia* (some could belong in subgenus *Austrosassia*), there can be little doubt that *S. nassariformis*, *S. sakuraii*, and *S. marshalli* are consubgeneric with *S. apenninica*.

Sassia (*Sassia*) *nassariformis* (Sowerby, 1902)

Lotorium nassariforme Sowerby, 1902: 95, pl. 2, fig. 7.

Argobuccinum (*Cymatiella*) *nassariforme*; Barnard, 1963: 24, fig. 3c (protoconch).

As interpreted here, this is another of the very widespread species of Cymatiidae with several widely disjunct geographic subspecies. In this case the specimens from different areas are almost inseparable, but slight differences in colour pattern and nodule size make recognition of subspecies desirable, although they are in need of further study. Taxa included in *S. nassariformis* are: *S. nassariformis nassariformis* (Sowerby), South Africa.

S. nassariformis remensa (Iredale) (Iredale 1936: 309, pl. 23, fig. 4, pl. 24, fig. 5), eastern Australia, and here recorded from northern New Zealand.

S. nassariformis semitorta (Kuroda & Habe in Habe) (Kuroda & Habe 1952: 76, *nomen nudum*; Kuroda & Habe in Habe, 1961: 46, pl. 23, fig. 4), southern Japan.

S. nassariformis n. subsp., relatively short, pale specimens dredged off Western Australia (in Western Australian Museum).

Sassia (*Sassia*) *nassariformis remensa* (Iredale, 1936)

Figs. 6, 13, 15-16.

Phanozesta remensa Iredale, 1936: 309, pl. 23, fig. 4, pl. 24, fig. 5; Garrard 1961: 14; Iredale & McMichael 1962: 55.

The single specimen examined from New Zealand is a freshly dead shell with a bright red-brown colour pattern, retaining much of the thin, straw coloured, sparsely bristled periostracum on the last whorl. It agrees in all details of shape, size, protoconch shape and sculpture, teleoconch sculpture, and aperture with specimens from New South Wales. It is surprising that this formerly Australian subspecies should not be taken in New Zealand waters until 1974, but no doubt the lack of previous collection is explained by the depth at which it lives, and the paucity of sampling at this depth around north-eastern New Zealand. New South Wales specimens have been recorded from 200 m (Iredale 1936, p. 309) and from 130 m and over (Garrard 1961, p. 14).

Dimensions: height 39.3 mm, diameter 18.3 mm.

Locality: N.Z. Oceanographic Institute stn. J709, 11/9/1974, 37° 15.2'S, 176° 50.0'E, central Bay of Plenty northwest of White Island, dredged in 328-406 m.

Sassia (*Sassia*) *marshalli* n. sp.

Fig. 9-11.

Shell small, elongate, with spire about equal to height of aperture plus siphonal canal. Whorls well inflated, lightly angled at the periphery by a faint spiral cord, but progressively less so down the shell. Sculpture of well raised, narrow-based, narrowly rounded, widely spaced collabral costae extending from suture to suture of spire whorls and onto the base of the last whorl, five in the last intervariceal space, six in the penultimate and seven in the antepenultimate intervariceal space; the whole surface crossed by numerous low, closely spaced, narrow, spiral threads, of which two or three on spire whorls and three or four on the last whorl are faintly more prominent than the others, and correspond to prominent cords of other species of *Sassia* (s. str.); 10 slightly more prominent threads on canal; all rendered microscopically cancellate by extremely numerous, fine, collabral threads over entire

surface. Siphonal canal short, weakly inclined towards the dorsum. Aperture oval, slightly larger than those of other species of *Sassia* (s. str.), with flared inner and outer lips, the inner edge of the outer lip bearing seven prominent denticles and the inner lip bearing a single prominent parietal ridge, margining a narrow posterior canal, and four weak ridges at the base of the columella. Varices arranged regularly at each two-thirds of a whorl, narrowly rounded, deeply hollowed, abaperturally, lacking nodules. Protoconch of three rounded whorls, bearing three low, narrow, widely spaced spiral cords that are evenly cancellated by low, narrow, widely spaced collabral costae. Colour medium orange-tan, with slightly darker, diffuse bands on a few spiral cords of the last whorl, and with small brown spots along the outer edges of terminal and earlier varices.

Dimensions: height 37.7 mm, diameter 19.2 mm (holotype).

Holotype (NZOI 231) and paratype (NZOI P326) in New Zealand Oceanographic Institute, Wellington.

Localities: N.Z. Oceanographic Institute stn. K844, 30° 11.2'S, 178° 33.8'W, off the Kermadec Islands in 290 m, 29/7/1974 (holotype); N.Z. Oceanographic Inst. stn. K826(3), 28° 48'S, 177° 48'W, N. of Raoul I., 390-490 m, 25/7/1974 (one fragmentary paratype).

The new species differs from all other Recent taxa of *Sassia* and from *S. apenninica* in lacking prominent spiral cords and the rows of small nodules where the cords cross the collabral costae, in having extremely narrow, well raised, "pinched" collabral costae, in having a slightly larger aperture and slightly more inflated whorls, and thus being proportionally wider, in having a shorter siphonal canal, and in its more subdued coloration; other Recent taxa have alternating light and dark spiral cords on a diffusely varied red-brown background, with dark red-brown patches on varices between the spiral cords, and with the same outer-lip spots as on *S. marshalli*. The combination of prominent, narrowly "pinched" collabral costae with very weak spiral sculpture makes this a highly distinctive shell.

The new species is named in honour of Mr Bruce Marshall, National Museum of New Zealand, who pointed out the new material in this paper to the writer, and who is monographing the molluscan fauna of the Kermadec Islands and Norfolk Ridge.

Subgenus *Proxicharonia* Powell, 1938

Charoniella Powell & Bartrum, November 1929: 426 (not *Charoniella* Thiele, October 1929 = *Negyrina* Iredalé, September 1929). Type species, (by original designation): *Charonia* (*Charoniella*) *arthritica* Powell & Bartrum, 1929, Lower Miocene, New Zealand.

Proxicharonia Powell, 1938: 373. Replacement name for *Charoniella* Powell & Bartrum, 1929, non Thiele.

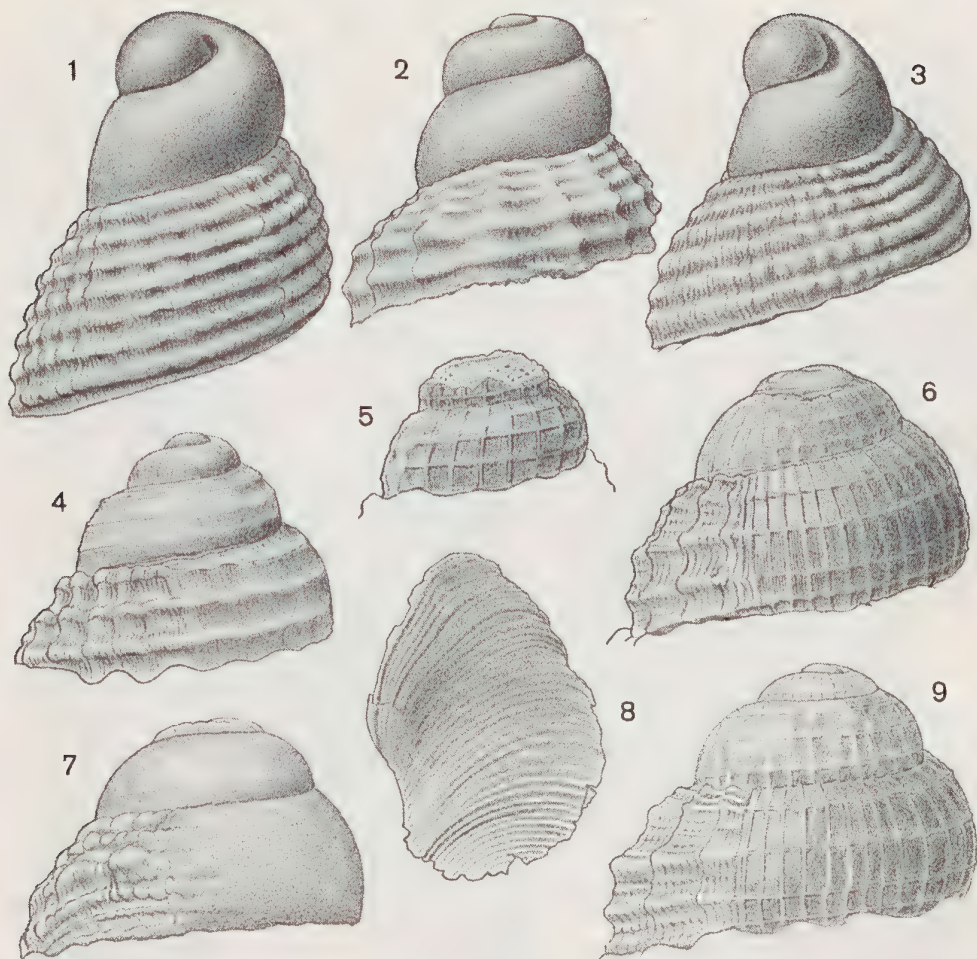
Sassia (*Proxicharonia*) *palmeri* (Powell, 1967)

Figs. 7, 26, 27.

Phroxicharonia palmeri Powell, 1967, p. 188, pl. 36, figs. 11, 12; Cernohorsky 1970, p. 187, fig. 2-5.

Sassia (*Proxicharonia*) *palmeri* has previously been recorded only from specimens taken by scuba divers at the Poor Knights Islands, New Zealand, and as a single shell found on the beach at Great Exhibition Bay, New Zealand, by Mr R. C. Willan. Six specimens can now be recorded from ridges to the north of New Zealand, five from near the Kermadec Islands and one from the Norfolk Ridge. The largest shell examined (Fig. 27) is 67 mm high, considerably larger than the largest of the 10 or so shells so far collected in New Zealand.

Cernohorsky (1970: 87, figs. 3-5) described an animal and figured the penis, operculum and radula of a Poor Knights Islands specimen of *Sassia* (*Proxicharonia*) *palmeri*, and pointed out that there are few differences between any of these features and those of *Sassia* (*Austrosassia*) *parkinsonia* (Perry). The protoconch of *Proxicharonia* has not been described previously, but worn ones remain on several of the present specimens, and similar but more eroded ones have been seen on a few New Zealand Lower Miocene specimens of *Proxicharonia*. The most complete available protoconch (Fig. 7) is turbiniform and smooth with well inflated whorls, and indistinguishable from that of *S. parkinsonia*. It is not possible to say whether any significant surface sculpture has been eroded from this protoconch, but none has been observed on any fossil or Recent specimens of *Proxicharonia*. The elongate, charoniiform shell shape is the only remaining criterion distinguishing *Proxicharonia* from the shorter, more prominently shouldered *Sassia* (*Austrosassia*), but as the two groups have been separate since at least Middle Eocene time in New Zealand, *Proxicharonia* should be maintained as a further subgenus of *Sassia*.



FIGURES 1-7, 9. Protoconchs of Cymatiidae and Cancellariidae, all enlarged X25.

1. *Semitriton dennanti* (Tate) (Cancellariidae), type species of *Semitriton* Cossmann; Glen Aire Clay, Point Flinders, west of Cape Otway, Victoria, Aldingan (Upper Eocene); WM 10589, N.Z. Geological Survey.
2. *Tatara revoluta* (Finlay) (Cancellariidae), GS 9841, Lorne, Waiareka Valley, Oamaru, New Zealand, Kaiatan (Upper Eocene); TM 5146, N.Z. Geological Survey.
3. *Semitriton varicosus* (Tate) (Cancellariidae), Browns Creek Clay, washout nearest Brown's Creek, Johanna, Victoria, Aldingan (Upper Eocene); P31009, National Museum of Victoria.
4. *Distorsio* (*Personella*) *septemdentata* Gabb, type species of *Personella* Conrad; Crockett Formation, Claiborne Group, Little Brazos River, Texas, Upper Eocene; WM5375, N.Z. Geological Survey.
5. *Distorsio* (*Distorsionella*) *lewisi* n. sp., paratype NZOIP323, N.Z. Oceanographic Inst. stn. 197, Wanganella Bank, Norfolk Ridge, 540-544 m.
6. *Sassia* (*Sassia*) *nassariformis remensa* (Iredale), type species of *Phanozesta* Iredale; 135 m, off Botany Bay, New South Wales, M.V. "Challenge"; WM 9319, N.Z. Geological Survey.
7. *Sassia* (*Proxicharonia*) *palmeri* (Powell), BS 307, between meteorological station and Hutchinson Bluff, Raoul I., 145-110 m, R.V. "Acheron"; MF24489, N.Z. National Museum.
9. *Sassia* (*Sassia*) *marshalli* n. sp., holotype, N.Z. Oceanographic Inst. stn. K84 4, off the Kermadec Islands, 290 m; NZOI 231, N.Z. Oceanographic Institute.

FIGURE 8. Operculum of *Distorsio* (*Distorsionella*) *lewisi* n. sp., paratype NZOI P324, locality as for Fig. 5 (enlarged X 12.5).

Localities: *Kermadec Islands* : BS307, between meteorological station and Hutchinson Bluff, Raoul I., 80-60 fm (145-110 m), R.V. "Acheron", 4/4/1973 (N.Z. National Museum, MF24489). BS309, off Bell's Flat, Raoul I., 120-190 fm (220-350 m), R.V. "Acheron", 4/4/1973 (N.Z. National Museum, MF 26360). BS437, bearing 338° T, 3.2 naut. miles off Fleetwood Bluff, Raoul I., 84 fm (154 m), R.V. "Acheron", 25/10/1975 (N.Z. National Museum, MF 25414). N.Z. Oceanographic Institute stn. K843, 30° 16.5'S, 178° 34.5'W, in 254-260 m, off Kermadec Islands, 29/7/1974. N.Z. Oceanographic Institute stn K869, 31° 21.6'S, 178° 53.0'W, in 285-390 m, off l'Esperance Rock, 1/8/1974.

Norfolk Ridge : N.Z. Oceanographic Institute stn. J705, 37° 16.0'S, 176° 51.0'E, Rangatira Knoll, in 190 m, 11/9/1974.

Genus *Fusitriton* Cossmann, 1903

Fusitriton Cossmann, 1903: 109. Type species (by original designation): *Triton cancellatus* Lamarck, 1816 (= *Neptunea magellanica* Röding, 1798), Recent, South America.

Fusitriton magellanicus laudandus Finlay, 1927

Prione retiolium; Finlay, 1924: 462 (not of Hedley, 1914).

Fusitriton laudandum Finlay, 1927: 399, pl. 20, fig. 65.

Fusitriton cancellatus laudandus; Beu, in press (synonymy, taxonomic revision).

Both *Fusitriton magellanicus* and *Cymatona kampyla kampyla* are common throughout central and southern New Zealand, and throughout southern and eastern Australia, at least as far north as northern New South Wales where, however, *F. magellanicus* is represented by the geographic subspecies *F. magellanicus retiolus* (Hedley). They have an optimum depth of about 300 to 600 m in the New Zealand region. In view of this depth and geographic distribution it is not surprising that both species occur in the deeper samples now being taken around the Kermadec Islands.

New Zealand Oceanographic Institute stn. K870, near l'Esperance Rock, Kermadec Islands, in 510-610 m contained, besides *Distorsio (Distorsionella) levisi*, two large, typical but broken shells of *Fusitriton magellanicus laudandus* Finlay, together with *Cymatona*, *Conus*, *Vexillum*, and *Gemmula*. Beu (in press) recorded *F. magellanicus laudandus* sparsely as far north as the Three Kings Islands and from one sample on the southern end of Norfolk Ridge, but this is the sole record from the Kermadec Islands.

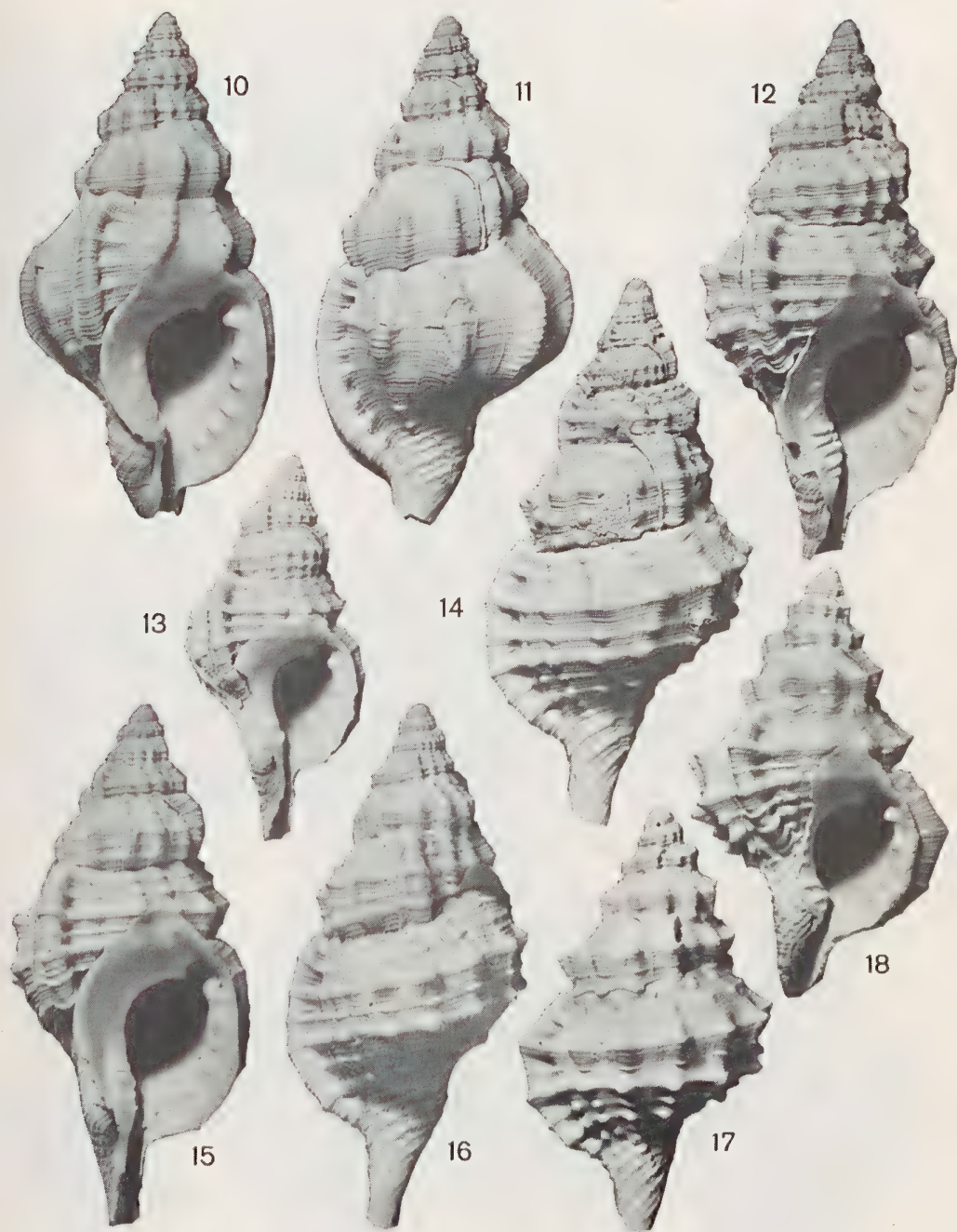
It is interesting that the Kermadec Islands specimens of *Fusitriton magellanicus* show the strong sculpture and weak, irregularly placed varices of the New Zealand subspecies *F. magellanicus laudandus*, and do not fall into the larger, more finely sculptured, and more coarsely and regularly varicate *F. magellanicus retiolus*. This suggests that the distribution of even this extremely widely dispersed taxon, with long-lived planktonic larvae, is controlled to some extent by continuity of submarine ridge systems.

Genus *Cymatona* Iredale, 1929

Cymatona Iredale, 1929: 177. Type species (by original designation): *Nassaria kampyla* Watson, 1883, Recent, New Zealand, eastern Australia, and the Kermadec Islands.

FIGURES 10-18. *Sassia* (sensu stricto) species, all enlarged X 2.

- 10, 11. *Sassia marshalli* n. sp., holotype, N.Z. Oceanographic Inst. stn. K844, off the Kermadec Islands, 290 m; NZOI 231, N.Z. Oceanographic Institute.
- 12, 14. *Sassia nassariformis semilorta* (Kuroda & Habe in Habe), Tosa Bay, Shikoku, Japan, 150 m; WM 11487, N.Z. Geological Survey.
13. *Sassia nassariformis remensa* (Iredale), type species of *Phanozesta* Iredale; immature specimen, 135 m, off Botany Bay, New South Wales; WM 9319, N.Z. Geological Survey.
- 15, 16. *Sassia nassariformis remensa* (Iredale), N.Z. Oceanographic Inst. stn. J709, northwest of White L., Bay of Plenty, New Zealand, in 328-406 m; N.Z. Oceanographic Institute.
- 17, 18. *Sassia apenninica* (Sassi), type species of *Sassia* Bellardi; Pliocene of Piedmont, Italy; WM 5358, N.Z. Geological Survey.



Cymatona kampyla kampyla (Watson, 1883)

Nassaria kampyla Watson, 1883: 594; Watson 1886: 405, pl. 14, fig. 12.

Cymatona kampyla kampyla; Beu, in press (synonymy, taxonomic revision).

New Zealand Oceanographic Institute stn. K870, near l'Esperance Rock, Kermadec Islands, in 510-610 m contained, besides the taxa listed above, a single complete, empty shell of *Cymatona kampyla kampyla*. Beu (in press) recorded the subspecies abundantly off eastern Australia and in southern New Zealand, most commonly in depths of 300 to 600 m, but specimens become progressively less common in northern New Zealand, and very few live specimens have been taken north of Cook Strait. However, it is not surprising that such a widely distributed taxon should occur sparsely at the Kermadec Islands.

Genus *Ranella* Lamarck, 1816

Ranella Lamarck, 1816: pl. 413. Type species (by subsequent designation, Children, 1823): *Ranella gigantea* Lamarck, 1816 (= *Murex olearium* Linnaeus, 1758), Miocene to Recent, Europe; Recent, Mediterranean - Atlantic - South Africa - New Zealand.

Reasons for regarding *Mayena* Iredale, 1917 as a synonym of *Ranella* Lamarck, 1816 were given by Beu (1976: 300).

Ranella olearia (Linnaeus, 1758)

Murex olearium Linnaeus, 1758: 748.

Ranella gigantea Lamarck, 1816: pl. 413, fig. 1.

Ranella olearium; Dell & Dance 1963: 162 (synonymy), pls. 16, 17.

Bursa barcellosi Matthews, Rios & dos Santos Coelho, 1973: 51, figs. 1-5.

The synonymy and distribution of this large, distinctive species were given by Dell & Dance (1963). The previously known distribution of Recent specimens is the Mediterranean Sea, the eastern Atlantic from off southern Ireland to Angola, the western Atlantic off Bermuda (H.A. Rehder, written commun.) and off Rio Grande do Sul, Brazil (Matthews *et al.* 1973, as *Bursa barcellosi*), off South Africa, St. Paul and Amsterdam Islands in the southern Indian Ocean (Arnaud & Beuoris 1972), and around northern New Zealand as far south as Banks Peninsula. Strangely, for a species that is presumably dispersed between South Africa and New Zealand as planktonic larvae, no specimens are known from Australia. This distribution pattern is made all the more incomprehensible by the present record of a single broken specimen of *Ranella olearia* from the southern Kermadec Ridge north of New Zealand.

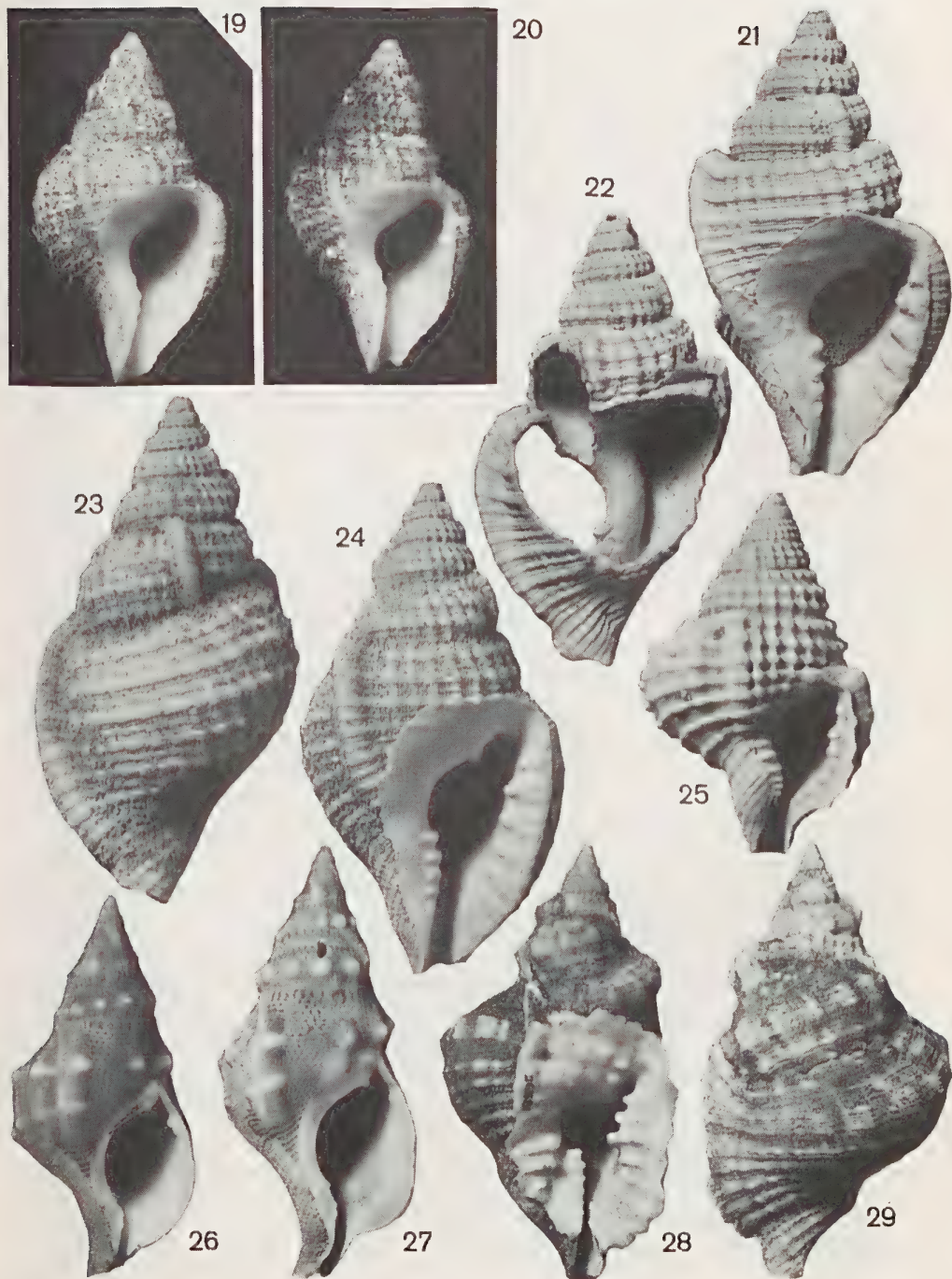
Locality: N.Z. Oceanographic Institute stn. K795, 33° 02.6'S, 179° 34.6'W, Star of Bengal Bank, Kermadec Ridge, 18/7/1974, in 270 m (with *Charonia lampas rubicunda*).

Subfamily Distorsioninae Kuroda, Habe & Oyama, 1971

The genitive form of *-torsio* (Latin: a wringing or gripping) is *-torsionis*, so a subfamily name based on *Distorsio* should be spelled Distorsioninae.

Figures 19-29.

- 19-24. *Distorsio* (*Distorsionella*) *lewis* n. sp., N.Z. Oceanographic Institute specimens enlarged X 2. Figs. 19, 20 - paratypes NZOI P323 and NZOI P324, collected with animals, N.Z. Oceanographic Inst. stn. 197, Wanganella Bank, Norfolk Ridge, 540-544 m. Figs. 21, 22 - paratype NZOI P325, N.Z. Oceanographic Inst. stn. K870, off l'Esperance Rock, Kermadec Islands, 510-610 m. Figs. 23, 24 - holotype, NZOI 230, N.Z. Oceanographic Inst. stn. P57, central Reinga Ridge, 563-614 m.
25. *Distorsio* (*Personella*) *septemdentata* Gabb, type species of *Personella* Conrad; unlocalised, Claiborne Group (Eocene) of Texas; WM 10585, N.Z. Geological Survey (enlarged X 3).
- 26, 27. *Sassia* (*Proxicharonia*) *palmeri* (Powell), off the Kermadec Islands, natural size. Fig. 26 - BS 307, between meteorological station and Hutchinson Bluff, Raoul I., 145-110 m; MF 24489, N.Z. National Museum. Fig. 27 - largest specimen, N.Z. Oceanographic Inst. stn. K843, east of Macauley and Curtis Islands, 254-260 m.
- 28, 29. *Distorsio* (*Distorsio*) *constricta habe* Lewis, BS 572, southeast of Smith Bluff, Raoul I., 82-100 m; MF 26581, N.Z. National Museum, natural size.



Genus *Distorsio* Röding, 1798Subgenus *Distorsio* sensu stricto

Distorsio Röding, 1798: 133. Type species (by subsequent designation, Gray, 1847): *Murex anus* Linnaeus, 1758, Recent, Indo-West Pacific.

Distortrix Link, 1807: 122. Type species (by subsequent designation, Dall, 1904): *Murex anus* Linnaeus, 1758.

Persona Montfort, 1810: 603. Type species (by monotypy): *Murex anus* Linnaeus, 1758.

Distorta Perry, 1811: pl. 2. Type species (by subsequent designation, Emerson & Puffer, 1953): *Murex anus* Linnaeus, 1758.

Distortio "Bolten" Gray, 1847: 133 (invalid emendation of *Distorsio* Röding, 1798).

Rhysema Clench & Turner, 1957: 236. Type species (by original designation): *Triton clathratus* Lamarck, 1816, Recent, Caribbean.

Lewis (1972) pointed out that *Distorsio burgessi* Lewis, 1972 and *D. perdistorta* Fulton, 1938 are intermediate in apertural features between *D. anus* and typical species of *Distorsio* (*Rhysema*) such as *D. clathrata* (Lamarck, 1816) and *D. reticulata* (Röding, 1798), and so synonymised *Rhysema* with *Distorsio* (sensu stricto).

Distorsio (Distorsio) constricta habei Lewis, 1972

Figs. 28, 29.

Distorsio (Rhysema) perdistorta; Habe, 1961: 46, pl. 23, fig. 1 (not of Fulton, 1938); Habe 1964: 74, pl. 23, fig. 1.

Distorsio constricta habei Lewis, 1972: 38, figs. 4, 10, 38, 39.

A single large specimen from the Kermadec Islands closely resembles *Distorsio constricta habei* Lewis, previously recorded from southern Japan only. Significant features of Japanese shells described by Lewis (1972), such as the pale orange-brown external colour, the closely spaced pair of peripheral spiral cords with a wider space below them, the sculpture of the inner and outer lips, the constriction of the siphonal canal by the anterior end of the outer lip, the extreme shell distortion, the presence of only 13 high, widely spaced collabral costae in each intervariceal space, and the short, fine periostracal bristles, are identical in the Kermadec Islands shell. The Kermadec specimen differs from Japanese ones only in its greater size, presumably having added a single growth step and varix beyond the size normally reached by Japanese specimens. No differences of taxonomic significance can be recognised.

Lewis (1972: 42) and Japanese authors have recorded the subspecies from south-eastern Japan only, from Boso Peninsula, Honshu to Tosa Bay, Shikoku, at depths of 100 to 200 m, and this would make an isolated Kermadec Islands record rather startling. However, the writer has examined other Pacific specimens of *Distorsio constricta habei*. Three Philippine Islands shells in the Western Australian Museum are typical, relatively small, strongly shouldered specimens of *D. constricta habei*: 52 fm, Panglao I., off Bohol I., Philippines, Mariel King on M.V. "Pele", 8/2/64 (2 specimens); 60-70 fm, Laoy I., off Bohol I., Philippines, 9/2/64 (1 specimen). Also seven small, immature shells in the Western Australian Museum from off northern Western Australia belong in a species distinct from the common *D. reticulata*, and seem referable to *D. constricta habei*: CSIRO stn. 17, 22° 59'S, 113° 25'E, SW of Pt. Cloates, Western Australia, 71 fm, 31/1/1964 (5 shells); CSIRO stn. 173, 21° 50'S, 113° 46'E, W. of Northwest Cape, Western Australia, 75 m, 6/10/1963 (1 shell); CSIRO stn. 187, 23° 39'S, 112° 11'E, S.W. of Pt. Cloates, Western Australia, 73 fm, 7/10/1963 (1 shell). So the apparent geographic separation of Japanese and Kermadec Island populations is not as wide as it seems at first, and probably *D. constricta habei* is widespread but uncommon in the western Pacific Ocean.

Dimensions of Kermadec I. shell: height 65.0 mm, greatest diameter 36.6 mm.

Locality: BS 572, 29° 18.9'S, 177° 56.4'W, south-east of Smith Bluff; Raoul I., in 82-100 m, R. V. "Acheron", 10 Nov. 1976 (N.Z. National Museum, MF 26581).

Subgenus *Distorsionella* n. subgen.

Type species: *Distorsio (Distorsionella) lewisi* n. sp.

The subgenus *Distorsio (Personella)* (Conrad 1865: 21) differs from *Distorsio* (sensu stricto) in its small size, its weakly distorted coiling, and its weakly armed aperture with only narrowly extended

columellar callus shield. Maxwell (1968) described a New Zealand Upper Eocene species and discussed the other members of the subgenus and their possible dispersal routes; almost all are Paleocene to Oligocene fossils, scattered sparsely around the world. Subsequently Cernohorsky (1975: 215, figs. 5-9) redescribed the only species referred to the subgenus in the living fauna, the very small Indo-West Pacific *D. (Personella) pusilla* Pease, 1861.

The species named below agrees in most features with the Eocene and Oligocene members of *Distorsio (Personella)*, but reaches a larger size and has a larger, more open, and even more weakly armed aperture than species of *D. (Personella)*; the aperture and base of the last whorl taper gradually into a long, broadly open siphonal canal, giving the shell a very different appearance from the sharply contracted base of *D. (Personella)*. The single protoconch remnant (Fig. 5) on the available specimens has widely spaced, fine, reticulate sculpture similar to that on the protoconch of *Sassia* (s. str.), whereas *D. pusilla* Pease has a smooth protoconch and the type species of *Personella*, *D. (Personella) septemdentata* Gabb, has a protoconch with narrow, widely spaced spiral cords but no prominent collabral sculpture (Fig. 4). The proboscis, radula and operculum of *D. lewisi* are very similar to those of *Distorsio* (s. str.). In summary, the relationships of the new species seem best expressed by placing it in the new subgenus *Distorsio (Distorsionella)*, differing from *D. (Personella)* in its reticulate protoconch, its widely open aperture and its long, tapering last whorl.

The new species *Distorsio lewisi* superficially resembles *Semitriton*. However, the type species of *Semitriton* Cossmann (Cossmann 1903, p. 102) (*Plesiotriton dennanti* Tate, 1898, Upper Eocene, Australia) has typically cancellariid columellar plaits and a tilted, paucispiral, smooth protoconch with a large inrolled apex and ends in a low varix, and so the genus belongs in the Cancellariidae near *Plesiotriton*. The other Australian Eocene species, *S. varicosus* (Tate, 1888) has a similar protoconch. Species of the New Zealand Eocene to Middle Miocene genus *Tatara* Fleming (Fleming 1950, p. 247; type species *Cymatium pahense* Marshall & Murdoch, 1921, Middle Eocene, New Zealand) are similar to *Distorsio lewisi* also, but have large columellar plaits of cancellariid type situated much higher up the columella than in *Distorsio (Distorsionella)*, and *Tatara* therefore belongs in the Cancellariidae near *Semitriton*. Protoconchs of *Semitriton* species (Figs 1, 3) and *Tatara revoluta* (Finlay) (Fig. 2) and a shell of *Distorsio (Personella) septemdentata* Gabb (Fig. 23) are included for comparison with those of *Distorsio (Distorsionella) lewisi*.

Distorsio (Distorsionella) lewisi n. sp.

Figs 5, 8, 19-24, 30A

Shell small, with spire slightly shorter than height of aperture plus canal. Whorls narrowly shouldered below upper suture, otherwise regularly and lightly convex; last whorl elongate, drawn out into a moderately long, widely open, gradually tapered siphonal canal. Varices well raised but narrow, weakly hollowed abaperturally, situated at each two thirds of a whorl. Sculpture of low, narrow, rounded spiral cords, three on spire whorls and seven on last whorl, the interspaces filled by numerous secondary and tertiary spiral threads; cancelled by low, narrow, rounded collabral costae at the same spacing as the spiral cords, with low, weak, nodules at the sculptural junctions, the whole surface crossed by numerous low, narrow collabral lamellae. Aperture large, long and narrowly triangular-ovate, with deeply excavated columella, and seven low denticles of almost even height (the uppermost smaller than those below it) inside the lightly flared outer lip; inner lip a thin callus spread a third of the way up the previous whorl, with a single large parietal ridge margining the wide posterior sinus, and with a row of four to six denticles on a callus pad at the base of the columella, the denticles decreasing in size down the columella as in other *Distorsioninae*. The upper two to three columellar denticles are continuous up the columella with the upper ones of previous apertures, forming extremely weak, very anteriorly placed columellar plaits. Protoconch (Fig. 5) not complete on any available specimen; broken remnant on larger paratype from stn. 197 turbiniform, with widely spaced, low, narrow spiral cords reticulated by widely spaced, low, narrow, collabral costae, as in *Sassia* (s. str.). Shell white. Periostracum light brown (wet) or pale straw-yellow (dry), a thin coating bearing dense, minute bristles, and sparse larger bristles, 1-2 mm long, at the sculptural junctions. Operculum (Fig. 8) irregularly quadrate-oval, small for aperture size, thin, pale yellow-brown, with curved growth ridges centred on right anterior corner, but lacking a nucleus. Proboscis long and slender, coiled in proboscis sheath (but not as extremely so as in *Distorsio* s. str.; Lewis 1972; fig. 14, 20-22), with extremely minute buccal mass at anterior end of proboscis; radula (Fig. 30A) minute (ca. 0.08 mm wide), with a short, wide, lightly curved

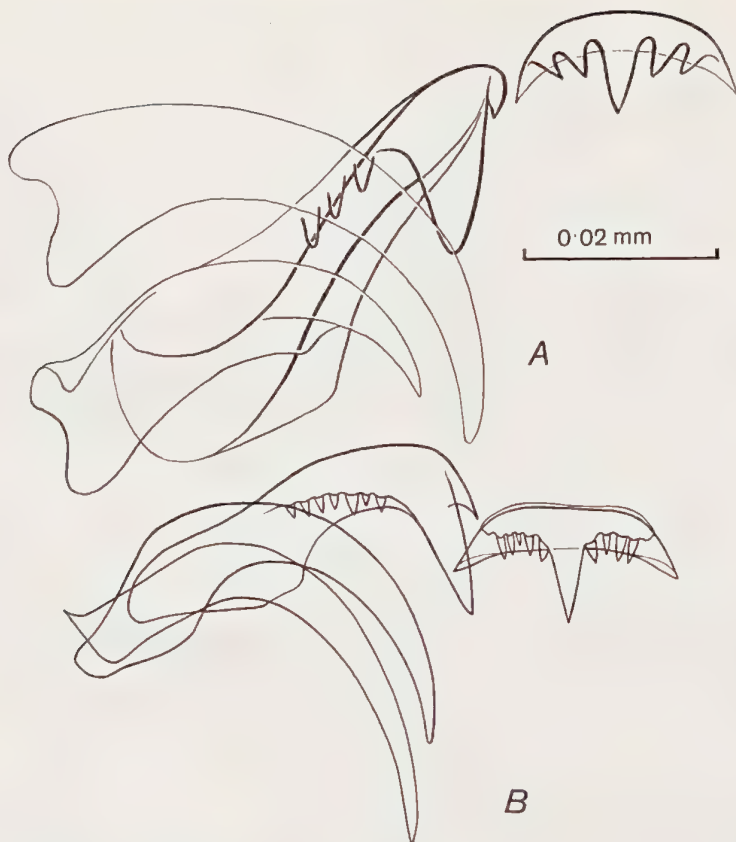


Figure 30. Radulae of *Distorsio*.

A. *Distorsio* (*Distorsionella*) *lewisi* n. sp., paratype NZOI P324, N.Z. Oceanographic Inst. stn. 197, Wanganella Bank, Norfolk Ridge, 540-544 m.

B. *Distorsio* (*Distorsio*) *anus* (Linnaeus), type species of *Distorsio* Röding; Plantation Reef, Marau Sound, Guadalcanal, Solomon Islands, coll. R.K. Dell; N.Z. National Museum (at markedly smaller scale than A).

central tooth having a large central cusp and two smaller lateral cusps, massive thick lateral teeth having a strongly hooked main cusp and an inner and three to four outer denticles, and two very thin, strongly hooked marginal teeth.

Dimensions: height 37.5 mm, diameter 19.8 mm (holotype); height 35.2 mm, diameter (incomplete) 19.3 mm (paratype, P325); height 26.4 mm, diameter 13.3 mm (smallest paratype, P323).

Holotype (NZOI 230) and three paratypes (NZOI P323-5) in New Zealand Oceanographic Institute, Wellington.

Localities: N.Z. Oceanographic Institute stn. P57, 33° 15.0'S, 169° 59.0'E, central Reinga Ridge (between northern New Zealand and Norfolk Ridge), 563-614 m, 4/2/1977 (holotype); N.Z. Oceanographic Institute stn. K870, 31° 21.2'S, 178° 44.5'W, 510-610 m, off l'Esperance Rock, Kermadec Islands, 2/8/1974 (broken adult paratype, P325); N.Z. Oceanographic Institute stn. 197, 32° 22.9'S, 167° 28.2'E, 540-544 m, Wanganella Bank, southern Norfolk Ridge, 25/7/1975 (two immature paratypes, P323-4, collected alive).

The obvious varices, long narrow aperture and extended last whorl, finely cancellate shell surface, strongly excavated columella, and base of the columella bearing an anteriorly decreasing row of ridges will make this shell readily recognisable.

The extremely minute buccal mass and radula proved difficult to recognise during dissection, and were found in only one of the dissected animals, and then by accident. The radula was examined and sketched (Fig. 30A) at X 625, at which power some details of cusp arrangement, and especially the structure of the base of the lateral teeth, could not be resolved. However, the general shape of the teeth and the position and relative sizes of most cusps were clear. The radula, and especially the central tooth, is similar to the much larger radula of *Distorsio* (*Distorsio*) *anus* (Linnaeus) (Fig. 30B).

The new species is named in honour of Mr Hal Lewis of Philadelphia, who has done so much to clarify the genus *Distorsio* (Lewis 1972) and who continues to be one of the few colleagues to appreciate the nuances of cymatiid taxonomy.

ACKNOWLEDGEMENTS

I wish to thank Mr F.W. Dawson, N.Z. Oceanographic Institute, and Dr F.M. Climo and Mr B. Marshall, N.Z. National Museum, for permission to describe material in their care, and Mr Marshall for pointing most of the material out to me. Mr T.A. Darragh, Deputy Director, National Museum of Victoria, Mr Hal Lewis, Department of Malacology, Academy of Natural Sciences, Philadelphia, and Dr P.A. Maxwell, N.Z. Geological Survey, commented on the manuscript. Drawings are by R. Brazier and photographs are by Miss D. Russell, both of N.Z. Geological Survey.

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BROODING OF CHITONS IN TASMANIA

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Tasmanian Museum and Art Gallery.

SUMMARY

The occurrence of brooding among Tasmanian chitons is reported. For *Ischnochiton (Ovatoplax) mayi* this habit is recorded for the first time. Notes of brooding by *Heterozona subviridis* and *Paricoplax crocinus* are included. Observations on *Eudoxoplax inornata* and *Callistasecla mawlei* suggest that these species may also brood.

INTRODUCTION

There has been very little research on the reproduction and development of chitons. However, it is known that there is a range from external fertilization of free eggs, through various stages of development in the parent's branchial cavity before discharge, to full development of juveniles before release and, ultimately, to viviparity (Dell, 1962 : 512-513; Smith, 1966: 433-466).

Although the occurrence of chitons brooding in Tasmania was first noticed in 1922, no further observations were made until 1971, when specimens of *Ischnochiton (Ovatoplax) mayi* were seen to have juveniles in the mantle cavity. In 1977, after the discovery of further species which either brooded or were suspected of doing so, it was decided that this aspect of chiton behaviour should be officially recorded.

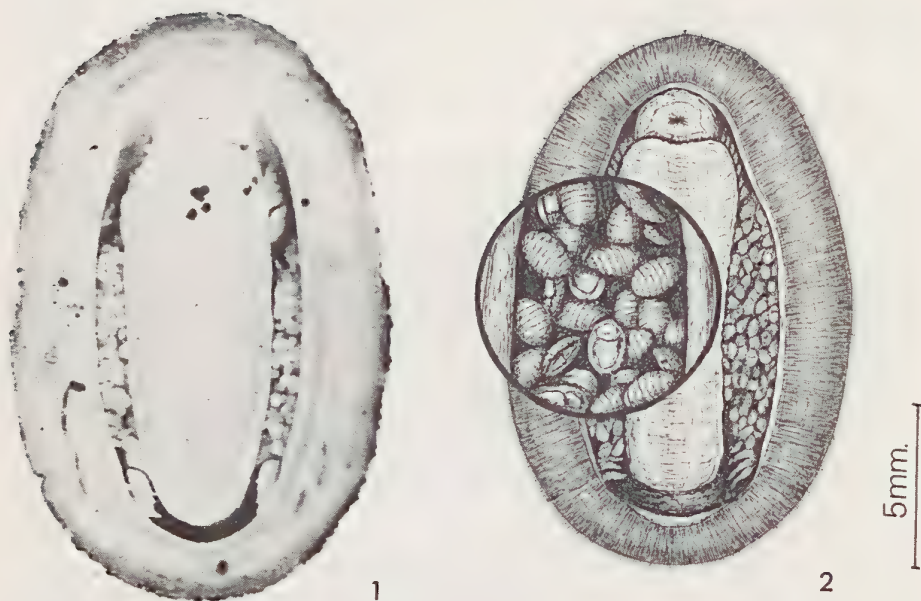
ABBREVIATIONS

A.N.S.P. Academy of Natural Sciences of Philadelphia.
N.M.V. National Museum of Victoria, Melbourne.
T.M. Tasmanian Museum, Hobart.

OBSERVATIONS

Ischnochiton (Ovatoplax) mayi

During April 1971, Mr. J.R. Penprase, of Hobart, collected 10 specimens of *Ischnochiton (Ovatoplax) mayi* Pilsbry, 1895, at Port Arthur, on Tasman Peninsula in south-eastern Tasmania. After their donation to the Tasmanian Museum (T.M. E8352), three were found to be brooding their young inside the mantle cavity. The latter range from well-developed eggs to metamorphosed (i.e. eight-valved) juveniles. An accurate count of numbers can not be taken unless the young are removed and it was decided not to disturb them at that time. However, estimates are:— specimen A, 30-40 on the left side of the foot and 20-30 on the right; specimen B, 30-40 on the left and none on the right; specimen C, none on the left and 50-60 on the right.



FIGURES 1-2.

1. Photograph of ventral view of *Ischnochiton (Ovatoplax) mayi* brooding 8-valved juveniles.
2. Drawing of *Ischnochiton (Ovatoplax) mayi* showing a magnification of juveniles.

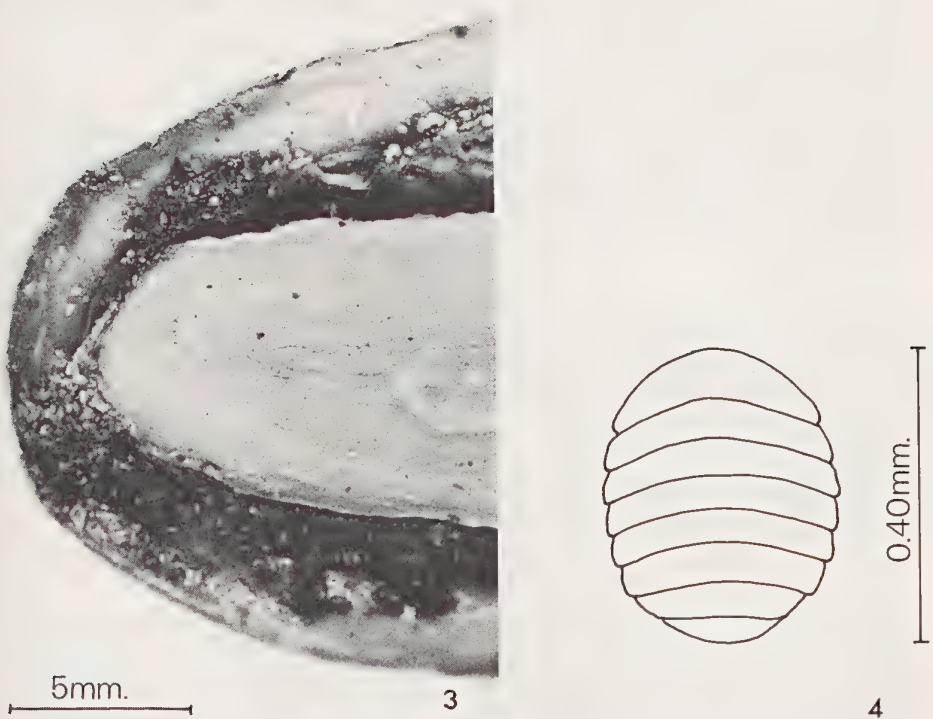
Examination of samples of *I.(O.) mayi* already in the Tasmanian Museum's collection revealed minute, metamorphosed juveniles still adhering to the dried valves of each of three specimens (T.M. E1277) which were collected in April 1957, from Point Puer, about two miles south of Port Arthur. The original positions of the young can not be ascertained, but their numbers are:— specimen D, three; specimen E, nine; specimen F, five.

Most *I.(O.) mayi* juveniles are about 0.80 mm. in length, while the parent adults range from 10-15 mm. However, three large, dry specimens (T.M. E187) from Maria Island, eastern Tasmania, collected in January 1917, by W.L. May, range in length from 13-17 mm. The remains of dried eggs are still attached inside the mantle cavity of the smallest of these three specimens.

Since April 1971, another seven samples of brooding *I.(O.) mayi* have been collected from south-eastern Tasmania:— Sadgrove Point (Bruny Island), May 1974 and November 1975; Dennes Point (Bruny Island), April 1977; Taranna, March 1975; Port Arthur, May and June 1971; Clyde Island (Eaglehawk Neck), September 1971.

The species was originally described by Pilsbry (1895: 128) and was placed in genus *Ischnochiton*, sub-genus *Haploplax*. It was recorded variously as *Ischnochiton (Haploplax) mayi* Pilsbry, 1895, or as *Sypharochiton mayi* (Pilsbry, 1895) until 1939, when Cotton and Weeding (1939: 184) established *Ovatoplax* as a new sub-genus of *Ischnochiton*, to contain this single species.

A series of syntypes of *I.(O.) mayi* is lodged in the Academy of Natural Sciences of Philadelphia (A.N.S.P. no 65626). These chitons were collected at Eaglehawk Neck, south-eastern Tasmania, by W.L. May on an unknown date. Of the five dried specimens, three show no sign of brooding whereas



FIGURES 3-4.

3. Photograph of ventral view of *Heterozona subviridis* brooding 8-valved juveniles.

4. Drawing of *Heterozona subviridis* juvenile.

the fourth has fifteen young still adhering to the valves and the fifth has thirty-six. (Dr. Robert Robertson, Academy of Natural Sciences of Philadelphia, personal communication, July 28, 1971). Pilsbry did not comment on this occurrence in his original description.

The syntype held by the Tasmanian Museum (T.M. E186), is a dried specimen represented only by the valves and it shows no sign of brooding.

Schnochiton (Ovatoplax) mayi prefers the undersides of rocks and stones, usually in sheltered bays and inlets. Localities where it has been found so far are Dover; Lunawanna, Barnes Bay, Sadgrove Point, Ford Point and Dennes Point (all on Bruny Island); Oyster Cove (D'Entrecasteaux Channel); Blackman's Bay; Spectacle Island (Frederick Henry Bay); Norfolk Bay; Taranna; Wedge Bay; Point Puer; Port Arthur; Fortescue Bay; Pirates Bay and Clyde Island (Eaglehawk Neck); Maria Island. *I.(O.) mayi* is also listed as being collected at Tamar Heads (May and Torr, 1912: 31). However, the author has not seen these examples, nor are they known to be lodged in any of the major museums of Australia, and it would be interesting to learn if they still exist. The species has not been recorded formally beyond the Tasmanian mainland. However, the Australian Museum, Sydney, has specimens collected from Clarke Island (Bass Strait) and Mallacoota (Victoria). (Dr. Winston F. Ponder, The Australian Museum, Sydney, personal communication, November 16, 1971).

Heterozona subviridis

Heterozona subviridis Iredale and May, 1916, a chiton found commonly in Tasmania, also broods its young to the eight-valved stage. Brooding was first recorded by Iredale and Hull (1923: 191), who stated: "One of us took specimens of *Heterozona subviridis* at King Island, Bass Strait, with clusters of eggs disposed along the outer margin of the foot".

Two specimens (T.M. E8357) of *H. subviridis* which were collected at Port Arthur, in February 1971, have many metamorphosed juveniles in the mantle cavity. The first chiton is 37 mm. in length and has over 100 young on the left side of the foot and more than 200 on the right. The second chiton, 40 mm. in length, has over 200 on the left side, but none on the right. The juveniles are 0.40 mm. long. A specimen (T.M. E8393), 23 mm. long, collected from nearby Safety Cove in February 1971, carries eight young. Another (T.M. E8367), 25 mm. in length, taken from Tinderbox, south of Hobart, in September 1971, broods six juveniles.

Paricoplax crocinus

Another chiton, *Paricoplax crocinus* (Reeve, 1847), broods its eggs, but it is not known as yet how far they develop before dispersal. One brooding specimen (N.M.V. G30097) was collected at East Devonport, north-western Tasmania, by Mr. R.C. Robertson, in December 1971. The eggs measure 0.30 mm. in length and are partially encased in a damaged, membranous sac. Without endangering the sac further, the number of eggs can not be ascertained, but is estimated at over 100. The brood is situated in the mantle cavity at the anterior end of the right side of the foot. The adult animal is 17 mm. long.

A dried specimen (T.M. E178) of *P. crocinus*, collected at Port Arthur in January 1917, by W.L. May, still has eggs adhering to the ventral surfaces of the valves.

Eudoxoplax inornata

An example (T.M. E9012) of the large chiton *Eudoxoplax inornata* (Tenison Woods, 1881), which can grow to a length of 100 mm., has been found with 20 loose, minute eggs in the mantle cavity on the left side of the foot. The adult animal measures 42 mm. and the eggs 0.20 mm. in length. It was collected at Tinderbox, southern Tasmania, by Mr. J.R. Penprase, in September 1974. Another specimen taken from Tinderbox in February 1971, shows dried eggs adhering to the ventral surfaces of the valves. However, it is not certain that *E. inornata* genuinely broods. Further specimens with eggs in the mantle cavity will need to be found to support these observations.

Callistasecla mawlei

An interesting species, but yet to be proven as a genuine brooder, is *Callistasecla mawlei* (Iredale and May, 1916). In a sample (T.M. E9675) from Port Arthur, collected in September 1976, by Mr. Penprase, metamorphosed juveniles are attached to the dorsal surfaces of the adults. Two specimens, 13 mm. and eight mm. long, which were donated to the Tasmanian Museum, each carry three young chitons. The latter have well-sculptured valves and are 0.30 mm. in length. Four adults from the same sample were retained by Mr. Penprase. There are 4-6 juveniles on the dorsal surface of each of these animals. However, 45-50 young are floating free in the alcohol in which the collection is preserved. Two half-grown chitons in the sample are not carrying any young.

CONCLUSION

It is apparent from Dell (1962: 513) and Smith (1966: 442) that few chiton species in the world are known to brood their young as far as the eight-valved stage. It is therefore significant that two such species, possibly three, should occur in Tasmania, with a further species, and probably another, brooding eggs. The author knows of no examples of brooding chitons found on the Australian mainland to date. Several brooding or viviparous echinoderms are also found in the waters of south-eastern Tasmania. The reasons for all of these cases of juvenile protection have not yet been ascertained.

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A special acknowledgement is due to Mr. J.R. Penprase, who collected many of the brooding specimens and who has greatly enlarged the chiton collection in the Tasmanian Museum by his donations of material.

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The Collector's Encyclopedia of Shells by S. Peter Dance, 1974, 288 pp., 2 text figures, 1 map, > 1500 coloured figures. First Australian edition, 1977; Australian & New Zealand Book Company Pty. Ltd.: Sydney. (ISBN 0-8552-071-X). Australian price \$17.95 (Copy supplied by: ANZ Book Co. Pty. Ltd., P.O. Box 459, Brookvale, N.S.W. 2100).

"The ever-growing interest in shell collecting in recent years has resulted in a spate of books popularising the subject, and the publication of yet another may seem superfluous." These introductory words from the preamble do sum up the situation. One cannot accept however that this particular book is superfluous. It is 288 pages of first class production – excellent text and superb illustrations.

The book encompasses only marine species of the world, with by far the greater part (194 pp.) devoted to the Gastropoda. The Bivalvia (53 pp.) are well represented, and the more specialized groups of Amphineura, Scaphopoda and Cephalopoda are more or less mentioned only in passing with 1½ pages each. The Introduction (7 pp.) concisely presents a wealth of essential information for the beginner and more advanced collector, covering briefly aspects of taxonomy, biology, growth, shell structure, form and ornament, colour and pattern, feeding, locomotion, and habitat, together with sections on collecting, preparation and storage, identification, distribution (with an easily understood map), and shell collecting past and present.

A great deal of care has been exercised in selecting the specimens photographed, and the camera work is of the same high standard throughout. Only one specimen appears to this reviewer to be of not choicest quality, that of the much sought-after *Conus gloriamaris*. Catering for the general collector, and no doubt with sales in mind, popular groups such as cowries (83 spp.), muricids (80 spp.) and cones (84 spp.) have a large coverage. Other attractive groups are well represented, cymatiids, mitres, volutes, larger marginellids, scallops and venerids each having more than 30 illustrations. Many other species are mentioned in the text, and are compared with species that are illustrated.

There are, as in every like book, problems of being out of date even before the very time of publication. In the five years from compilation to this Australian edition, a number of systematic revisions have appeared, each necessitating a number of taxonomic changes. The result of one such revision, for example, means that in the genus *Penion* (pp. 140-1), entries should be altered to read: for *grandis* Gray and *oligostira* Tate read *mandarinus* Duclos; for *mandarinus* Duclos read *sulcatus* Lamarck.

No doubt there are taxa in the book that need to be changed for other reasons. For instance, Australian malacologists regard the chiton on p.26 as as the subspecies *Ischnochiton elongatus crispus* and its distribution as New South Wales and far-eastern Victoria. They would prefer to call the *Turbo* on p.51 by the earlier taxon *gruneri* Philippi. They would recognize also *Guildfordia triumphans* (p.50) as occurring in north-eastern Australian seas. And the list would run on, and on, as the specialists each add information for a particular region.

But no matter what complaints and objections may be raised regarding the book, there can be no doubts that it is a visually delightful reference to use. This Australian edition of Peter Dance's *The Collector's Encyclopedia of Shells* is very highly recommended to all shell collectors from beginners to specialists.

Robert Burn

FURTHER STUDIES ON THE DEGENERATION OF MONOAMINE NERVES IN THE VENUS CLAM HEART INDUCED BY NEUROTOXIC DRUGS: EFFECTS OF 5,7-DIHYDROXYTRYPTAMINE (5,7-DHT).

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SUMMARY

The long term effects of 5,7-DHT on nerves in the Venus clam heart were studied to elucidate further the structure of serotonergic nerves detected earlier.

At least 2 types of monoaminergic nerves with dense-cored vesicles were susceptible to significant degeneration by the drug. Among these were profiles with large granular vesicles (64-200 nm) which resemble possible serotonergic nerves seen in myenteric plexus and 'catch' muscle of *Mytilus*. The other nerves lesioned were those with small granular vesicles (32-64 nm) conforming to adrenergic nerves in vertebrates. A third type of profile with a population of medium-sized, dense-cored vesicles (40-160 nm) was found to be reactive and less susceptible to degeneration.

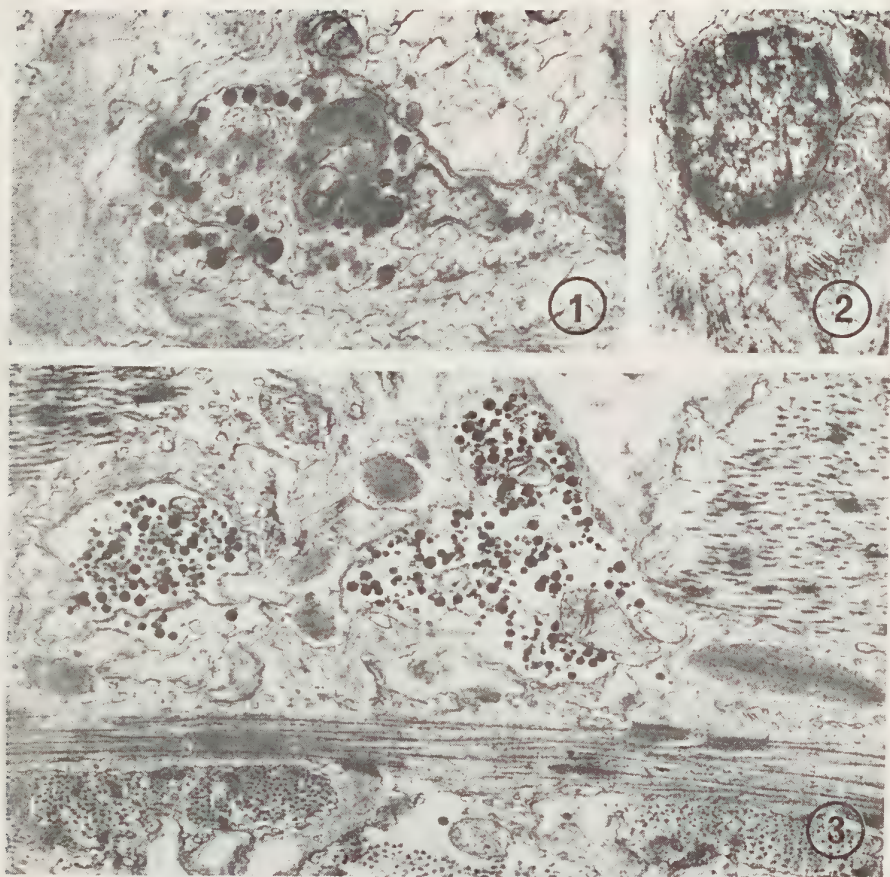
Nerves with a predominance of small agranular vesicles and large opaque vesicles were unaffected by the drug. These resemble vertebrate cholinergic and "purinergic" nerves, respectively.

The results confirm our previous studies on the molluscan heart with neurotoxic drugs.

Key words: Venus clam heart - *Katelysia rhytiphora* (Mollusca) - 5,7-Dihydroxytryptamine - 5-Hydroxytryptamine - Dopamine - Electron microscopy

INTRODUCTION

An earlier communication (Sathananthan & Burnstock, 1976) reported some degeneration of monoamine nerves in the heart of the Venus clam, induced by 5,6-Dihydroxytryptamine (5,6-DHT). Among these, were profiles with large granular vesicles (LGV) that were reactive to this drug and suspected to be serotonergic. 5,6-DHT also caused significant degeneration of similar nerves in *Mytilus* 'catch' muscle (Sathananthan, 1976).

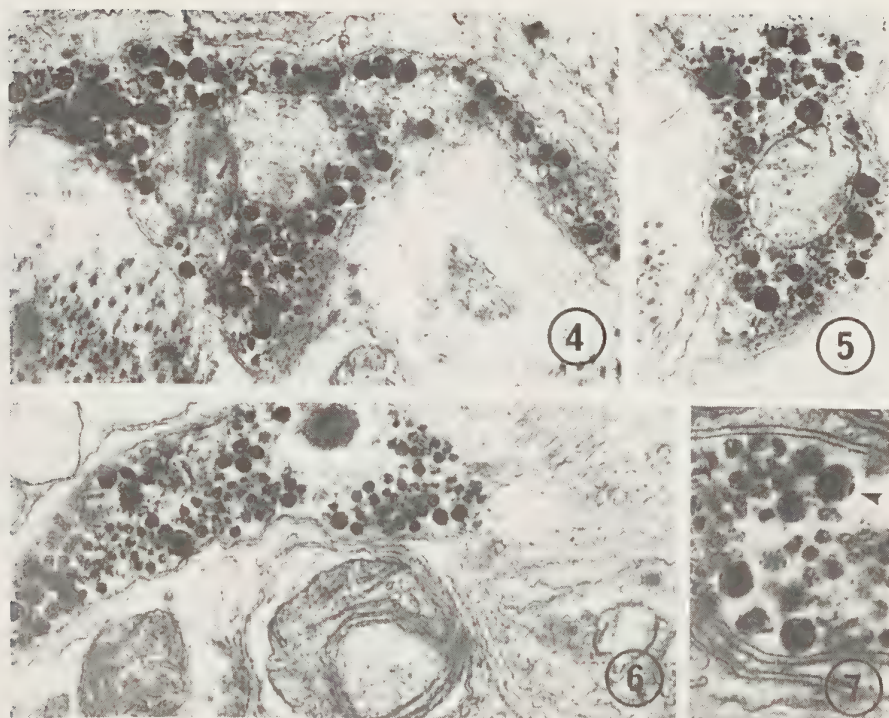


FIGURES 1-4. Electron micrographs of nerves in the clam heart after treatment with 5,7-DHT (8 days).

1. Degenerating non-terminal axon containing LGV (80-180 nm), some of which are enclosed in myelin-like membranes while others appear less electron-dense or degranulated. X28,000.
2. Non-terminal axon with ghosts of predominantly SGV (32-64 nm) and a few LGV (80-96 nm) in a denser axoplasm. X27,300.
3. Reactive profile containing MGV (40-140 nm) close to muscle. The larger vesicles have lost their haloes while the smaller vesicles have acquired cores indicating uptake of the drug. X15,400.

The dihydroxytryptamines are now being widely used in neurotoxic studies in mammals (see Baumgarten et al., 1974; Björklund et al., 1974), and 5,7-DHT is thought to be an improvement on 5,6-DHT in the lesioning of indoleamine nerves (Baumgarten & Lachenmayer, 1972). 5,7-DHT also produced extensive lesioning of possible serotonergic (5-HT) nerves in the myenteric plexus of *Mytilus* (Sathananthan, 1977a).

This paper deals with the long term effects of 5,7-DHT on nerves in the clam heart and a further attempt is made to establish the ultrastructural identity of 5-HT nerves in molluscs.



FIGURES 4-7

4. Terminal axon with reactive MGV (48-140 nm) wedged between muscle fibres forming close myoneural junctions. Note distorted mitochondria and denser axoplasm. X28,000.
5. Reactive terminal axon (vesicles 40-180 nm) between muscle fibres. X28,000.
6. Reactive axon (vesicles 40-160 nm) in a multiaxonal profile showing partial degeneration. An unreactive axon is seen on the right. X28,000.
7. Nerve with reactive vesicles showing denser crescents (arrow) and fine granules associated with their membranes. X51,000.

MATERIALS AND METHODS

Young venus clams, *Katelysia rhytiphora*, were collected and treated with 2.5×10^{-4} gm/ml 5,7-DHT as outlined in our previous study (Sathananthan & Burnstock, 1976). After 8 days of drug treatment, the hearts were fixed in 4% glutaraldehyde in 0.1M cacodylate buffer (pH 7.3) containing 8% sucrose (2 hr) followed by fixation in 1% OsO₄ (1 hr) and embedded in Araldite. Sections (≈ 70 nm thick) were cut with a Reichert OMU3 ultramicrotome, stained with alcoholic uranyl acetate and alkaline lead citrate and examined with a Philips 301 electron microscope.

RESULTS

The appearance of various nerve types in controls and after short-term treatment with 5,6-DHT and 6-OHDA were reported earlier (Sathananthan & Burnstock, 1976). Axons were sometimes associated with Schwann-like cells and were often accompanied by glial processes. Multiaxonal profiles with different types of axons and nerves forming close myoneural junctions were commonly seen in this study.

DRUG EFFECTS

After 8 days treatment with 5,7-DHT well marked degenerative changes were noted in monoamine nerves, particularly in those with LGV, confirming our earlier observations with 5,6-DHT (Sathananthan & Burnstock, 1976). There were evidently two populations of LGV - one more susceptible to degeneration while the other was reactive and rather resistant to degeneration. Apart from these nerves, there were also profiles with small granular vesicles (SGV) that were also lesioned.

The profiles with LGV that showed significant degeneration (Fig. 1) had vesicles (64-200 nm), distorted mitochondria, dense polymorphic and multivesicular bodies resembling lysosomes and phagosomes, respectively. Most of the LGV had lost their haloes and some appeared less electron-dense or degranulated. Clumps of LGV enclosed by myelin-like membranes were also seen.

The nerves that were most reactive to the drug were widely distributed and contained a range of medium-sized, granular vesicles (MGV), 40-160 nm, with many large vesicles (Figs. 3-7). Their axoplasms were often denser and the vesicles had lost their haloes or acquired specks or blobs of more electron-dense material and appeared to be labelled rather than loaded. Thus, their overall appearance seemed to be somewhat different to those nerves with LGV that were susceptible to degeneration by 5,7-DHT in this and previous studies where the material was processed in the same manner (Sathananthan, 1977a). Closer examination revealed that even smaller vesicles were granulated while some of the larger ones had 1 or 2 denser crescents associated with their membranes (Fig. 7). A few vesicles, both large and small, also had eccentric cores. The reactive axons were rather resistant to degeneration although a few showed signs of partial degeneration with clumps of vesicles (Fig. 6) or dense bodies.

The degenerating nerves with SGV (32-64 nm) showed typical signs of dark degeneration characteristic of catecholamine nerves. These profiles were either uniformly dense and revealed faint outlines of vesicles or had ghosts of SGV and a few LGV in a dense axoplasm (Fig. 2). Many were embedded in muscle and often associated with groups of muscle mitochondria.

Two types of nerve profiles remained unaffected by the drug. Of these, one had a predominance of small agranular vesicles (SAV), 40-70 nm, and were rare, while the other had large opaque vesicles (LOV), 80-200 nm, and were quite common and often large.

Apart from the above nerve types, there were large axons with only mitochondria and irregular specks of granular material resembling glycogen or huge profiles with numerous mitochondria packed with a heterogeneous population of LGV. Purkinje-like fibres similar to those found in the mammalian heart were also seen in the auriculoventricular junction of this clam heart.

DISCUSSION

The evidence presented confirms our earlier suspicions that nerve profiles in the molluscan heart containing LGV could possibly be serotonergic (Sathananthan & Burnstock, 1976). In fact, there seem to be two populations of large dense-cored vesicles that react differently to 5,7-DHT - one showing a greater susceptibility to degeneration than the other. Whether these represent two types of monoaminergic nerves is debatable.

The profiles that showed substantial degeneration resemble possible serotonergic nerves containing LGV identified with the dihydroxytryptamines in *Mytilus* 'catch' muscle and gut (Sathananthan, 1976, 1977a). All these nerves had dense-cored vesicles (56-200 nm) with a predominance of LGV. Similar degenerating nerves were also observed after treatment with 5,7-DHT in the myenteric plexus of this Venus clam (Sathananthan, 1977b) and in the CNS of *Helix* (Sathananthan, in preparation), where many of the axons had numerous degranulated LGV (65-225 nm). Such nerves could be serotonergic as there is also histochemical, biochemical and physiological evidence to indicate that 5,7-DHT is neurotoxic for indoleamine nerves in the snail brain (Osborne & Pentreath, 1976). Further, axons with LGV (> 200 nm) were labelled with radio-active 5-HT in the CNS of *Helix* (Pentreath, 1976).

The axons with MGV that were less susceptible to degeneration but reactive, appeared to be loaded, suggesting uptake of the drug. The maximum diameter of these vesicles was usually ~ 160 nm although one or two vesicles measured up to ~ 180 nm. Axons with a similar population of vesicles were lesioned by 6-OHDA (personal communication) and these could be catecholaminergic. Comparable profiles with medium-sized granular vesicles (56-130 nm) were found to show less degenerative changes with 5,7-DHT in the myenteric plexus of *Mytilus* (Sathananthan, 1977a) but these were different in their overall vesicular appearance. Axons with reactive MGV were also

seen in the brain of *Helix*, side by side with nerves containing degranulating MGv, after injection of 5,7-DHT (Sathananthan, in preparation). Pentreath (1976) labelled similar nerve terminals with MGv (~ 100 nm) in the CNS of *Helix*, by injecting radioactive 5-HT. Whether the reactive profiles represent catecholaminergic or serotonergic nerves needs to be clarified by further study.

The degenerating axons with SGV resemble adrenergic nerves commonly seen in vertebrates. Similar nerves were affected by both 6-OHDA and 5,6-DHT in this heart (Sathananthan & Burnstock, 1976) and were thought to be dopaminergic. The dihydroxytryptamines lesion both serotonergic and adrenergic nerves in vertebrates (see Baumgarten et al, 1974; Bjorklund et al, 1974). The pharmacological, biochemical and histochemical evidence available indicates that 5-HT and DA are the possible monoaminergic neurotransmitters in the nervous system of bivalves, whereas evidence for the involvement of noradrenalin is lacking (see Sathananthan & Burnstock, 1976; for a detailed discussion). Therefore it seems logical to conclude that the two types of nerve profiles with LGV and SGV could represent serotonergic and catecholaminergic nerves in these molluscs.

The profiles with SAV that were not lesioned by 5,7-DHT conform to cholinergic nerves of vertebrates. Acetylcholine is now well established as a molluscan neurotransmitter and similar profiles with SAV were seen in our previous studies (Sathananthan & Burnstock, 1976; Sathananthan, 1976, 1977a). A further type of nerve terminal seen in all our studies with molluscan neurones were those with a predominance of LOV which resemble "purinergic" nerves in the vertebrate gut (see Burnstock, 1975). These findings confirm the presence of a non-cholinergic, non-monoaminergic innervation in this mollusc (Sathananthan & Burnstock, 1976), where the heart was seen to be sensitive to ATP and nerves with LOV were found to be unaffected by both 6-OHDA and 5,6-DHT and showed Mg-ATPase and 5'-nucleotidase activities.

ACKNOWLEDGEMENTS

The author thanks the Royal Children's Hospital, Royal Melbourne Institute of Technology and Lincoln Institute for research facilities.

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THE NOMENCLATURE OF THREE PACIFIC *BULLA* SPECIES

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SUMMARY

The correct nomenclature is established for *Bulla quoyii* Gray in Dieffenbach, 1843, *Bulla angasi* Pilsbry, 1893 and *Bulla vernicosa* Gould, 1859. Full synonymies are given as well as descriptions and locality records.

INTRODUCTION

Now that comparative anatomical and ecological studies are being made on species of *Bulla* it has become critical to re-evaluate the abundance of earlier literature to stabilize the taxonomy of the common species of this important cephalaspidean genus. There has been considerable taxonomic confusion over the names of all the reasonably widespread species as evidenced by the 20 proposed specific names for the 3 valid species dealt with here.

Not only has there been a plethora of specific names but until recently there has been no unanimity regarding the most appropriate generic taxon itself. This confusion arose because Linneaus (1758) first used *Bulla* as a subgenus of *Gryllus*, an orthopteran insect (p. 427), and only subsequently (p. 725) introduced it for a large series of molluscs. Later authors have therefore used all of the 5 following alternative names to designate this genus *sensu lato*: *Bullus* Montfort, 1810; *Bullaria* Rafinesque, 1815; *Bullea* Blainville, 1825; *Vesica* Swainson, 1840; *Quibulla* Iredale, 1929 (Dall, 1908; Iredale, 1929; Thiele, 1931; Pruvot-Fol, 1954; Abbott, 1954; 1974), although some have since been challenged or relocated. It is most fortunate that the name *Bulla* Linneaus, 1758 has now been conserved by the International Commission on Zoological Nomenclature (Opinion 196, 1954) with the type-species by designation under the Plenary Powers: *Bulla ampulla* Linneaus, 1758.

This publication examines the nomenclature of only 3 species of *Bulla* which are found in the Pacific Ocean. No synonymies have been attempted for other widespread Pacific species (e.g. *Bulla ampulla* Linneaus, 1758; *Bulla punctulata* A. Adams in Sowerby, 1850) or more restricted species (e.g. *Bulla peasiana* Pilsbry, 1893 with type from Hawaii or *Bulla tenuissima* Sowerby in Reeve, 1868 with type from Swan River, West Australia) which occur in the Pacific area.

TAXONOMY

BULLA QUOYII GRAY IN DIEFFENBACH, 1843

Figures 15-24

- 1825 *Bulla australis* Gray, *Ann Philos* (New Series) 9: 408 [Australia]; 1827. Gray, in Capt. King's *Survey of Aust* 2 Appendix: 490, No. 92; 1835. Gray, in Yates' *Account of New Zealand* Appendix: 308; 1843. Gray, in Dieffenbach, *Trav. N.Z.* 2: 243, No. 114 [New Zealand]; 1885. Brazier, *Proc Linn Soc. N.S.W.* 10(1): 89-91; 1903. Pritchard & Gabriel, *Proc Roy Soc Victoria* 15 (New Series) 2: 176-223 (non *Bulla australis* Ferrussac, 1822).
- 1833 *Bulla striata* Quoy and Gaimard, *Voy. l'Astrolabe Zool.* 2: 354, pl. 26, figs. 8, 9 [Bay of Islands, New Zealand and Jervis Bay, New Holland] (non *Bulla striata* Bruguière, 1792).
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- 1843 *Bulla quoyii* Gray, in Dieffenbach, *Trav. N.Z.* 2: 243 [New Zealand]; 1874. E.A. Smith, *Voy. Erebus & Terror Zoology* 1839-1843 2: 5; pl. 1, fig. 11.
- 1850 *Bulla oblonga* A. Adams in Sowerby, *Thes. Conchyl.* 2: 577, No. 50, pl. 123, fig. 74 [Philippines and Anna Is.=error]; 1854. H. & A. Adams, *Gen. Rec. Moll.* 2: 16; 1867. Angas, *Proc Zool. Soc. Lond.* : 226, No. 257; 1868. Sowerby in Reeve, *Conch. Icon.* 16, pl. 3, sp. 9, figs. a-c; 1873. Hutton, *Cat. Mar. Moll. N.Z.* : 244; 1877. Tenison-Woods, *Proc Roy Soc. Tasmania* : 47; 1880. Hutton, *Man. N.Z. Moll.* : 121.
- 1850 *Bulla castanea* A. Adams in Sowerby, *Thes. Conchyl.* 2: 584, No. 78a, pl. 124, fig. 106a [Shores of New Zealand].
- 1853 ?*Bulla* (*Bullea*) *substriata* Menke, *Zeit. f. Malakozool.* 10(9): 136 [New Holland].
- 1873 *Bulla quoyi* Gray, Hutton, *Cat. N.Z. Moll.* : 52, No. 245; 1880. Hutton, *Man. N.Z. Moll.* : 121; 1893. Pilsbry, *Man. Conch.* 15: 348, pl. 39, fig. 71.
- 1893 *Bulla australis* var. *oblonga* A. Adams, Pilsbry, *Man. Conch.* 15: 346-347; pl. 35, figs. 12-14.
- 1893 *Haminea castanea* A. Adams, Pilsbry, *Man. Conch.* 15: 374; Pl. 41, fig. 14.
- 1913 *Bullaria australis* Quoy & Gaimard, Suter, *Man. N.Z. Moll.* : 534; 1915. Suter, *Atlas*, pl. 49, fig. 6 (non *Bulla australis* Ferrussac, 1822).
- 1913 *Bullaria australis quoyi* Gray, Suter, *Man. N.Z. Moll.* : 535
- 1918 *Bullaria botanica* Hedley, *J. Proc. Roy. Soc. N.S.W. Suppl.* 51: M 104, No. 1104 (substitute name for *Bulla australis* Gray, 1825); 1958. May and MacPherson, *Ill. Index Tasmanian Shells*: 50, pl. 46, fig. 14; 1962. MacPherson and Gabriel, *Mar. Moll. Victoria*: 242, fig. 281.
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- 1937 *Vesica quoyi* Gray, Powell, *Shellfish N.Z.* (1st ed.): 84 (Fam. Bullidae)
- 1946 *Quibulla quoyi* Gray, Powell, *Shellfish N.Z.* (2nd ed.): 88 (Fam. Vescicidae); 1957. Powell, *Shells N.Z.* (3rd ed.): 111 (Fam. Bullidae); 1961. Powell, *Shells N.Z.* (4th ed.): 103; 1968. Morton & Miller, *N.Z. Sea Shore*: 543, fig. 202 (5); 1970. Rudman, *J. nat. Hist.* 5: 657-662, pls 8-12 (anatomy); 1970. Penniket, *N.Z. Seashells in Colour*: 68, pl. 31, fig. 2 (labelled fig. 4 in error).
- 1965 *Bulla* (*Quibulla*) *quoyi* Gray, Powell, *Rec. Auck. Inst. Mus.* 6(2): 167, pl. 22, fig. 10
- 1966 *Bulla botanica* Hedley, Burn, *Mem. Nat. Mus. Vict.* 27: 266; 1975. Coleman, *What Shell is that?* 14 (fig. 9).

REMARKS: The taxonomic confusion over the name of this species stems not only from Gray's (1825) and Quoy and Gaimard's (1833) independent introduction of the preoccupied taxon *Bulla australis*, but also that both Gray and Quoy & Gaimard proposed two names each: *Bulla australis* and *Bulla quoyii* of Gray (1825; 1843); *Bulla striata* and *Bulla australis* of Quoy & Gaimard (1833) all being introduced without adequate diagnosis or comparison. Brazier (1885) recognised that *B. australis* Gray and *B. australis* Quoy and Gaimard were conspecific and gave a full synonymy without referring to, or amalgamating, *B. quoyii* Gray or *B. striata* Quoy & Gaimard. Pritchard and Gabriel (1903) repeated the greater part of this synonymy but maintained "*Bulla quoyi* A. Adams" from New Zealand as a separate species. Other names that fall into synonymy are *Bulla oblonga* A. Adams in Sowerby, 1850, *Bulla castanea* A. Adams in Sowerby, 1850, *Bulla substriata* Menke, 1953 and *Bulla botanica* (Hedley, 1918), the latter having been introduced in a check list without description. It is this name which has become entrenched in Australian literature (Iredale, 1929; MacPherson & Gabriel, 1962; Allan, 1962; Iredale & McMichael, 1962; Burn, 1966; Coleman, 1975) whilst the combination "*Quibulla quoyi* (Gray, 1843)" has been consistently used in New Zealand works (Powell, 1946 et seq.; Morton & Miller, 1968; Rudman, 1970; Penniket, 1970).

Pilsbry (1893) tentatively placed *Bulla substriata* Menke in the synonymy of *Bulla australis* Gray, this synonymy may be correct, however since the type is lost it cannot be checked. Menke (1853)

himself admitted *substriata* was probably the same as *B. striata* Quoy & Gaimard but he had no access to their works to enable comparison.

The spelling of the name must revert to *quoyii*, in accordance with I.C.Z.N. article 32(a) since this is the correct original spelling of Gray in Dieffenbach, 1843.

TYPES: Following correspondence with Miss A. Blake of the Mollusca Section of the British Museum (Nat. Hist.) I have ascertained that the following type lots are held in that institution. Ten syntypes of *Bulla quoyii* are present (Reg. Nos 1842 11 18 135-142), these having been received from Mr Stranger. The largest syntype (Reg. No. 1842 11 18 135) was figured by E. A. Smith (1874). Three syntypes of *Bulla oblonga* A. Adams in Sowerby are present (Reg. No. 197647). The probable holotype of *Bulla castanea* A. Adams in Sowerby is in the Lombe-Taylor Collection (Reg. No. 1881 5 20 22). This shell was purchased from Sowerby in 1881, it fits the figure and was originally labelled: "*castanea* - unique". However A. Adams in Sowerby does not state the source of his figured shell so it cannot be certain that this is the holotype.

DESCRIPTION: Adult size varies from 15 to 55 mm, shell thin, ovoid, whorls moderately convex; shell narrowed posteriorly and expanded anteriorly; apical cavity deep with sides slanting and reasonably perspective, revealing $4\frac{1}{2}$ - 5 involute whorls; posterior edge of outer lip rises sharply above level of apical cavity, anterior portion of outer lip smoothly rounded. Shape and size are very variable (Willan, 1977). A smooth white callus is closely applied to the umbilical region and a thin opaque glaze extends from this callus the length of the parietal wall.

On the base of the shell are 9-24 incised spiral lines, with the SEM these lines resolve into an overlapping series of chisel-shaped punctae; these spirals are conspicuous on early whorls (*i.e.* on the ventral side of the body whorl) becoming weaker on the dorsal side of the last half whorl in adult shells. These spirals are virtually absent behind the outer lip in some of the largest shells the author has examined from New South Wales, Australia.

Occasionally one or two obsolete spiral lines are present near the apex; sculpture on spire whorls inside the apical cavity is of up to 5 incised spirals and occasional axial ribs on early whorls; some shells display an external pattern of gently undulating longitudinal flattened ridges (Fig. 20). Details of sculpture of the spiral lines and apical cavity have been presented elsewhere (Willan, *op. cit.*).

Shell colouration is of mottlings of purplish-grey, browns and white (Fig. 17); sometimes the whites and browns are arranged in irregular longitudinal streaks (Fig. 22); beach shells often take on a superficial milky-grey hue; in juvenile shells the mottlings can be orange-brown in colour; near-vertical walls of spire whorls are white in colour, although the apex of each whorl is brown. Mature shells may have a whitish glaze inside the outer lip and there may be a thickened white ridge parallel to the lip itself, the extreme edge of the outer lip is brown. Live shells are covered with a thin olive to orange-brown periostracum.

Details of anatomy have been given by Rudman (1970; 1971).

HABITAT: *Bulla quoyii* burrows in sand, which can be either fine or moderately coarse in texture, although the mollusc prefers a moderate silt fraction. *B. quoyii* is thus frequently found in conjunction with *Zostera* but individuals are occasionally found in intertidal pools amongst coralline turf. Subtidally the species is nocturnal, numerous live specimens have been seen on night SCUBA dives but never during the day.

LOCALITY RECORDS: NEW ZEALAND: Cape Maria van Diemen Beach; Pananehe Island, Spirits Bay; Pukenui Wharf area, Houhora Harbour; Paxton Point, Great Exhibition Bay; Kohotutea Point, near Cape Karikari; "The Lagoon", Cape Karikari; Main Beach, Mahinepua, near Whangaroa (all RCW); Waewaetoria Island (Coles Coll.); Motuarohia (Robertson) Island (RCW); Rawhiti Beach; Long Beach, Bay of Islands (both AIM); Bland Bay and Whangaruru Harbour; Tutukaka Harbour; Passage Island, southern side of Whangarei Harbour entrance (all RCW); Uikuhart's Bay, Whangarei Heads (AIM); Goat Island Bay, Ti Point, Matheson Bay, Leigh; Opahi Bay, Mahurangi Heads west; Waiwera Beach; Tiritiri Matangi Island; Army Bay and Shakespear Beach, Whangaparaoa Peninsula (all RCW); Takapuna Beach and Rangitoto Island; Cheltenham Beach; Howick Beach, Cockle Bay, Orakei Basin (all AIM); Beachlands Beach (RCW); Surfdrive Beach, Waiheke Island (AIM), Waihou Bay, near Cape Runaway (RCW); Bark Bay, Nelson (RCW). QUEENSLAND: Trinity Bay (Hodge coll.). NEW SOUTH WALES: Shellharbour (AIM); Coogee (Hodge Coll.); Long Reef, near Manly (RCW); Bottle and Glass Rocks, Watsons Bay and Port Jackson (AIM; AWBP; RCW); Kurnell, Botany Bay (AWBP; RCW); Gunnamatta Bay, Port Hacking (RCW); Garie Beach; Bellambi Beach (both RCW). VICTORIA: Rosebud, Port Philip; Portland (both AIM). SOUTH AUSTRALIA: The Grange (RCW);

Outer Harbour, Adelaide (AIM); Stansbury (AWBP); Semaphore Beach (AWBP); Henley Beach (AWBP). TASMANIA: North Coast and Furneaux Group (May & MacPherson, 1958). S.W. AUSTRALIA: King George Sound and Princess Royal Harbour, Albany (Quoy & Gaimard, 1832).

DISCUSSION: Although *Bulla quoyii* exhibits greater variability than the other species examined here, it stands apart from all other Pacific bubble shells not only because of the basal spiral striae but also because of its light weight and relatively open umbilical cavity. Adult shells of *B. quoyii* are larger in size in Australia. Suter (1913) listed "coasts of the North Island . . . also Australia and Tasmania" as the range of "*Bulla australis* Quoy and Gaimard". Iredale (1929) recognised the presence of spiral lines in "*Quibulla botanica*" and recalled that this feature had hitherto been considered a character solely of New Zealand specimens.

BULLA ANGASI PILSBRY, 1893

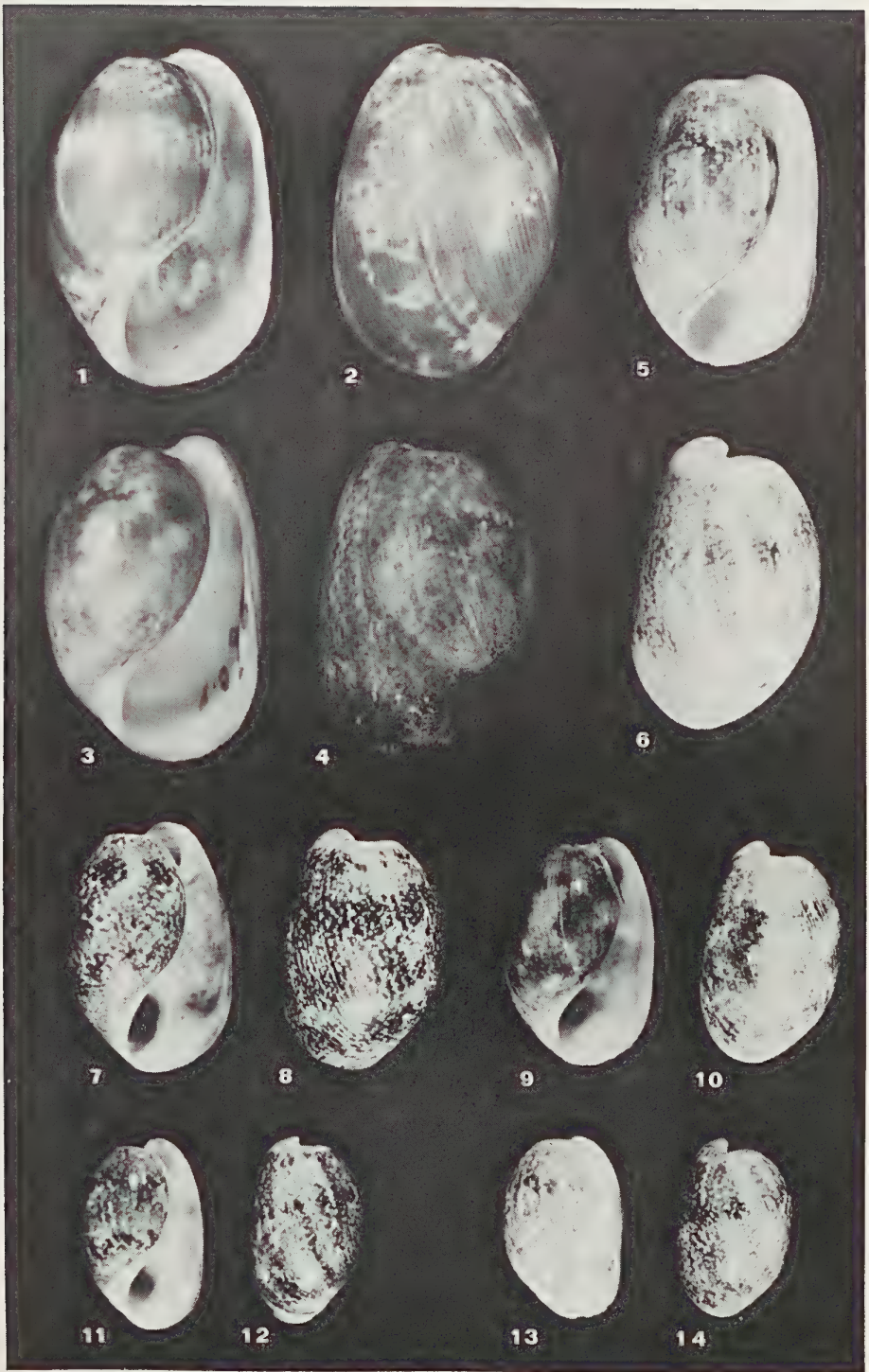
Figures 1-2, 25-37

- 1867 *Bulla solida* Gmelin, Angas, *Proc. Zool. Soc. Lond.*: 226 = No. 259 [Middle Harbour, Port Jackson]; 1868. Sowerby in Reeve, *Corch. Icon.* 16, pl. 4, figs. 10a, b [Hab.:?] (non *Bulla solida* Gmelin, 1791; nec Bruguiere, 1792)
- 1867 *Bulla magdelus* "Lister", Angas, *Proc. Zool. Soc. Lond.*: 227, No. 260 [Middle Harbour, Port Jackson] (nom. nud.)
- 1867 *Bulla ovulum* Gould, Angas, *Proc. Zool. Soc. Lond.*: 227 [Middle Harbour and Long Bay] (published erroneously in synonymy of "*Bulla magdelus* Lister").
- 1893 *Bulla angasi* Pilsbry, *Man. Conch.* 15: 347, pl. 36, figs. 32, 33 (substitute name for *Bulla solida* Sowerby in Reeve, 1868 and "*Bulla solida*" Angas, 1867 from Middle Harbour, Port Jackson).
- 1906 *Bulla adamsi* Menke, Suter, *Trans. N.Z. Inst.* 39: 265 [Cape Maria van Diemen, N.Z.] (non *Bulla adamsi* Menke, 1850).
- 1913 *Bullaria adamsi* Menke, Suter, *Man. N.Z. Moll.*: 534; 1915. Suter, *Atlas*, pl. 49, fig. 6 (non *Bulla adamsi* Menke, 1850).
- 1915 *Bullaria peasiana* Pilsbry, Oliver, *Trans. N.Z. Inst.* 47: 542 [Kermadec Islands] (non *Bulla peasiana* Pilsbry, 1893).
- 1918 *Bullaria punctulata* A. Adams, Hedley, *J. Proc. Roy. Soc. N.S.W. Suppl.* 51: M 104, No. 1106 [New South Wales] (non *Bulla punctulata* Adams in Sowerby, 1850).
- 1929 *Quibulla angasi* Pilsbry, Iredale, *Aust. Zool.* 5(4): 350, pl. 38, fig. 8 [Sydney Harbour].
- 1937 *Quibulla scotti* Iredale, *Aust. Zool.* 8(4): 258, pl. 16, fig. 11 [Lord Howe Island].
- 1937 *Quibulla ovulum* Angas, Iredale, *Aust. Zool.* 8(4): 258 [Sydney Harbour]; 1962. Iredale & McMichael, *Mem. Aust. Mus.* 11: 88, No. 1854.
- 1965 *Bulla (Quibulla) subtropicalis* Powell, *Rec. Auck. Inst. Mus.* 6(2): 167, pl. 22, figs. 8, 9 [type locality Norfolk Island; also in N.Z.].
- 1970 *Quibulla subtropicalis* Powell, Penniket, *N.Z. Seashells in Colour*: 68, pl. 31, fig. 3.
1971. *Bulla subtropicalis* Powell, Rudman, *J. nat. Hist.* 5: 662, 663 (anatomy).
- 1976 *Bulla vernicosa* Gould, Powell, *Rec. Auck. Inst. Mus.* 13: 159 [Cape Maria van Diemen to Whangarei Heads, N.Z.] (non *Bulla vernicosa* Gould, 1859).

REMARKS: Consideration of the most appropriate name rests on interpretation of the homonymous taxa "*Bulla solida* Gmelin" Angas, 1867 and *Bulla solida* Sowerby in Reeve, 1868. Pilsbry (1893) proposed the substitute name *A.* (that is *Bulla*) *angasi* for both *B. solida* Sowerby (1868) from unknown locality and "*B. solida* Gmelin" as of Angas (1867) from Middle Harbour, Port Jackson, Australia. Sowerby's specimen of *B. solida* is in the British Museum (Nat. Hist.), London, but Angas' specimen can no longer be traced. Since Pilsbry's substitute name was based on two different specimens, one from unknown locality and the other from Middle Harbour, it is

FIGURES 1-14.

- 1, 2. *Bulla angasi* Pilsbry, lectotype (= syntype of *Bulla solida* "Adams MS", Sowerby in Reeve, 1868. 35.3 x 23.7 mm. (British Museum Nat. Hist. 197646).
- 3, 4. *Bulla vernicosa* Gould, figured syntype of *Bulla ovula* "Gould", Sowerby in Reeve, 1868. 33.2 x 23 mm. (British Museum Nat. Hist. 197645).
- 5, 6. *B. vernicosa* Gould, Erakor Lagoon, Efate Island, New Hebrides. 46.3 x 29.8 mm.
- 7, 8. *B. vernicosa* Gould, Rarotonga Island, Cook Group. 38.2 x 26.5 mm. (Hodge Coll., Zoology Department, University of Auckland).
- 9, 10. *B. vernicosa* Gould, Tanna Island, New Hebrides. 35.5 x 23.7 mm.
- 11, 12. *B. vernicosa* Gould, Okinawa Island, Ryukyu Group. 29.6 x 19.8 mm. (Hodge Coll., Zoology Department, University of Auckland).
- 13, 14. *B. vernicosa* Gould, Luganville foreshore, Espiritu Santo Island, New Hebrides. 28.9 x 19.9 mm.



taxonomically advisable to select the only remaining syntype of Sowerby's *B. solida* as the lectotype of *B. angasi* Pilsbry. The lectotype of *B. solida* Sowerby (= *angasi* Pilsbry) (Figs. 1, 2) is in the British Museum (Nat. Hist.), Reg. No. 197646; length 35.3 mm, width 23.7 mm.

Angas (1867) used the invalid, mis-spelt and pre-Linnean name "*B. magdelus* Lister" for this species and in error included "*B. ovulum* Gould MS." in synonymy. The species "*B. ovula* Gould MS" as of Sowerby in Reeve, 1868, is actually the tropical Pacific species *B. vernicosa* Gould, 1859. Iredale's (1937) resurrection of the name "*B. ovulum* Angas" for the Sydney Harbour species is therefore inappropriate since this specific name designates an entirely different species which apparently does not occur at Sydney.

Iredale (1937) introduced *Quibulla scotti* for the Lord Howe Island population and also one dead shell from Elizabeth Reef and distinguished them from the Sydney Harbour forms, but the differences are no greater than those between New Zealand and Norfolk Island shells and can be encompassed within the limits of variation of *Bulla angasi*. The holotype of *Quibulla scotti* is in the Australian Museum (Reg. No. C60245) but there is some doubt as to its validity. Iredale states that the type is from Lord Howe Island and gives its dimensions as 40 x 27 mm but none of the material from Lord Howe Island in the Australian Museum approaches that size. On the other hand the shell from Elizabeth Reef is close in size (38 x 25.05 mm) and there is a note in the register dated 21 May 1937 in Iredale's own handwriting giving it as type. The figure given by Iredale closely matches this shell. So it would appear as though the specimen from Elizabeth Reef was intended as holotype of *Quibulla scotti* and Iredale got his localities confused (Ponder, *pers. comm.*). The holotype of *Bulla (Quibulla) subtropicalis* Powell is in the Auckland Institute and Museum (Reg. No. TM-1245), this name being a replacement for "*Bullaria peasiana* Oliver" from Norfolk Island, the Kermadecs and northern New Zealand.

DESCRIPTION: Shell moderately small (largest specimen examined 33 mm) solid and heavy, cylindrical; apical cavity a minute, straight-sided perforation. Posterior edge of outer lip rises above level of apical cavity; outer lip bends inward medially and is constricted posteriorly so that the outer lip runs parallel to the shell's longitudinal axis; the upper part of the aperture is therefore narrow; basally the outer lip is moderately expanded and rounded. A porcelain white callus covers the umbilicus and a thin glaze extends the length of the parietal wall; in fresh shells the underlying pattern remains visible through this glaze.

Shell smooth, there are no basal spiral lines, but incised spirals are present on the spire whorls in the apical cavity; the only external sculpture that can be present are longitudinal growth lines (Fig. 26).

Colouration is variable, generally consisting of a close mottling of chocolate or reddish-brown on a paler ground and clouded with small or large splotches of darker brown; occasional shells display a "punctulate" pattern (Figs. 29-31) reminiscent of *Bulla punctulata* A. Adams in Sowerby, but this pattern is never maintained with the consistency or accuracy of that species. Darker encircling bands can sometimes be distinguished; apical cavity white. Interior of aperture with a white glaze giving the shell its solidity; a thickened ridge is present parallel to the basal part of the outer lip but disappears medially where the outer lip bends inward. Figs. 32, 33 illustrate a New Zealand shell with a colour pattern reminiscent of that of the lectotype.

The morphology of the radula and gizzard plates has been described by Rudman (1971) who found the anatomy of the soft parts to be very similar to *B. quoyii*.

HABITAT: *B. angasi* appears to live only subtidally and apparently only in habitats of relatively clean sand. Live specimens have been found on a mixed substrate of shell sand and coral gravel with small algae at Slaughter Bay, Norfolk Island (Rudman, 1971), these specimens were found at night crawling over the sediment surface in 4-5 m of water (R.V. Grace, *pers. comm.*). The present author has taken one specimen, which although dead still contained the animal, it was partially buried in coarse sand at the depth of 5 m at Matapouri Beach, Northland, New Zealand.

LOCALITY RECORDS: NEW CALEDONIA: Amadée Island, off Noumea; Thio (both RCW). NORFOLK ISLAND: (specimens in Coles Coll.; Hodge Coll.; AIM; AWBP; Hole Coll.; RCW coll.). NEW SOUTH WALES: Hungry Head, near Urunga; Long Reef, near Manly, Watsons Bay. Port Jackson (all RCW); Shellharbour, Kurnell, Botany Bay (AWBP); Elizabeth Reef (Iredale, 1937). LORD HOWE ISLAND: (Iredale, 1937). NEW ZEALAND: Cape Maria van Diemen Island (AIM); Cape Maria van Diemen Beach (AWBP; Hodge Coll.); Pananehe Island and Spirits Bay (Coles Coll.; Douglas Coll.; RCW); North Head and Paua Pt, Parengarenga Harbour (Douglas Coll.); Paxton Point,

Great Exhibition Bay (RCW); Rarawa Beach, southern end of Great Exhibition Bay (Coles coll.); Kohotutea Point, near Cape Karikari (RCW); Waewaetoria Island, Bay of Islands (Coles Coll.); Bland Bay, Whangaruru Peninsula; Matapouri Beach; Rocky Bay, Tutukaka Harbour; McGregors Bay, Whangarei Heads (all RCW); Great Barrier Island (AWBP) Mokohinau Islands (M. Mika Coll.); "Waterfall Reef" and "Echinoderm Reef", near Goat Island; Western side of Goat Island; Matheson Bay, Leigh (all RCW). KERMADEC ISLANDS: Raoul Island (AWBP); Denham Bay, Raoul Island (Douglas Coll.). WESTERN SAMOA: Beach 20 miles from Apia (Hole coll.).

DISCUSSION: Shells from New South Wales are indistinguishable from New Zealand material. Shells from the Norfolk Island population (type locality of *Bulla subtropicalis* Powell, 1965) are significantly larger ($P < 0.001$) having a mean length of 25.81 mm ($n = 37$) than those from New Zealand (mean length = 20.46 mm; $n = 34$) but specimens from these localities agree in other characters.

Cernohorsky (1972) placed *Bulla angasi* (as *B. subtropicalis* Powell) in the synonymy of *B. vernicosa* Gould; but *B. angasi* is more closely related to *B. punctulata* A. Adams in Sowerby and were it not for the sympatric existence of both *B. angasi* and *B. punctulata* in New Caledonia and Western Samoa one could consider the possibility of them being subspecies. A comparison of *B. angasi* and *B. vernicosa* is given in the discussion on the latter species.

BULLA VERNICOSA GOULD, 1859

Figures 3-14

- 1850 *Bulla australis* Quoy & Gaimard, A. Adams in Sowerby, *Thes. Conchyl.* 2(1): 576, pl. 127, figs. 64-66; 1868. Sowerby in Reeve, *Conch. Icon.* 16, pl. 4, figs. 12 a-c [Tahiti]; 1878. Brazier, *Proc. Linn. Soc. N.S.W.* 2(1): 83 [N.E. Australia, Islands of Torres Straits] (non *Bulla australis* Quoy & Gaimard, 1833).
- 1859 *Bulla vernicosa* Gould, *Proc. Boston Soc. nat. Hist.* 7: 138 [Loo Choo (Ryukyu) Islands]; 1862, Gould, *Otia Conch.*: 111; 1893. Pilsbry, *Man. Conch.* 15: 349; 1936 Hirase, A. *Coll. of Jap. Shells* (5th ed.): 90, pl. 118, fig. 12; 1950. Habe, *Ill. Cat. Jap. Shells*: 21, fig. 2; pl. 3, fig. 16; 1962. Kira, *Shells W. Pac. in Colour*: 114, pl. 40, fig. 13; 1972. Cernohorsky, *Mar. Shells Pac.* 2: 207, pl. 59, fig. 4.
- 1868 *Bulla ovula* "Gould", Sowerby in Reeve, *Conch. Icon.* 16, pl. 2, figs. 5a, b [Locality unknown].
- 1885 *Bulla adamsi* Brazier, *Proc. Linn. Soc. N.S.W.* 10(1): 92 (substitute name for *Bulla australis* A. Adams in Sowerby, 1850) [Tahiti, N.E. Australia, Torres Straits] (non *Bulla adamsi* Menke, 1850).
- 1893 *Bulla adamsi* Menke, Pilsbry, *Man. Conch.* 15: 345, pl. 35, figs. 15, 16, 19, 20; 1961. Rippingale & McMichael, *Qid and Gt Barrier Reef Shells*: 151, pl. 21, fig. 4; 1975. Coleman, *What Shell is That?*: 183, fig. 518 (non *Bulla adamsi* Menke, 1850).
- 1893 *Bulla vernicosa* var. *ovula* (Gould) Sowerby, Pilsbry, *Man. Conch.* 15: 349, pl. 36, figs. 34, 35.
- 1909 *Bullaria adamsi* Menke, Hedley, *Aust. Assoc. Adv. Sci.*: 370 [Queensland] (non *Bulla adamsi* Menke, 1850).
- 1938 *Bullaria (Bullaria) adamsi* Menke, W. Adam & LeLoup, *Rés. Sci. Voy. Indes. Orientales Néerlandaises*: 197 (non *Bulla adamsi* Menke, 1850).
- 1962 *Quibulla adamsi* Menke, Allan, *Aust. Shells*: 119 (footnote) (non *Bulla adamsi* Menke, 1850).
- 1965 *Bulla adamsii* Menke, Guang-Yu & Si, *Oceanologia Limnol. Sin.* 7(1): 2, pl. 1, fig. 1 (non *Bulla adamsi* Menke, 1850).
- 1966 *Bulla ovulum* Angas, Burn, *J. Malac. Soc. Aust.* 9: 96, figs. 1-4 [Southern Queensland] (non "*Bulla ovulum* Gould", Angas, 1867).

REMARKS: A future monograph on the genus may consider *Bulla vernicosa* Gould, 1859 to be insufficiently described since the original diagnosis is inadequate and there is no designated type. Some recent workers (Adam & LeLoup, 1938; Rippingale & McMichael, 1961; Allan, 1962; Guang-Yu & Si, 1965; Coleman, 1975) have followed Pilsbry (1893) in incorrectly using the name *Bulla adamsi* (or its unjustified emendation *adamsii*) Menke, 1850 for this tropical Pacific species. However the type locality of *B. adamsi* Menke is Mazatlan, Mexico and American authors place *B. adamsi* Menke in the synonymy of *B. punctulata* A. Adams in Sowerby, 1850 (Carpenter, 1872; Keen, 1971; Abbott, 1974).

Bulla adamsi Brazier, 1885 was a replacement name for *B. australis* A. Adams in Sowerby, 1850 an earlier preoccupied name for *B. vernicosa* Gould. Brazier was unaware his name was homonymous with *B. adamsi* Menke, 1850.

The name *Bulla ovulum* was never published by Gould (Johnson, 1964) and was therefore first validly published by Sowerby in Reeve, 1868, with the Loo Choo (= Ryukyu) Islands as type locality. Three syntypes (including the figured syntype) of *B. ovulum* Sowerby in Reeve are in the British

Museum (Nat. Hist.) Reg. No. 197645, and all are conspecific with *B. vernicosa* Gould. I have illustrated Sowerby's figured syntype in Figs. 3, 4.

The author has examined the *ex-pisces* shell from the Capricorn Group, one of two shells referred to "*B. ovulum* Angas" by Burn (1966) and finds it to be a rather elongate, and immature specimen of *Bulla vernicosa*. Burn's other shell from Rainbow Bay, Coolangatta is, judging by its description and illustration, also *B. vernicosa* Gould.

DESCRIPTION: Adult size up to 45 mm (a population of 27 adult shells from Luganville, Santo Island, New Hebrides had a mean length of 26.07 mm). Shell solid, globose, whorls convex; widest part of the shell near the middle, apical cavity moderately open and perspective, revealing 5-6 involute whorls. A white columellar callus is present but it is not totally reflected back onto the shell and leaves a narrow crescentric umbilical chink; a thin whitish or translucent glaze covers the parietal wall.

Shell smooth and polished, without any basal incised lines but up to 6 microscopic spirals are present on the involute whorls of the spire in the apical cavity; the only external sculpture is of numerous, close, longitudinal folds. Basic colouration is of a fine mottling of light brown and white over the whole shell, there can be 2-4 encircling bands of darker brown although the apical area is always lightly mottled, the apical cavity itself is white, fresh shells always have a highly polished, glazed external appearance. Interior of the aperture is thickened and white, adult shells have a low white ridge just inside the inner lip.

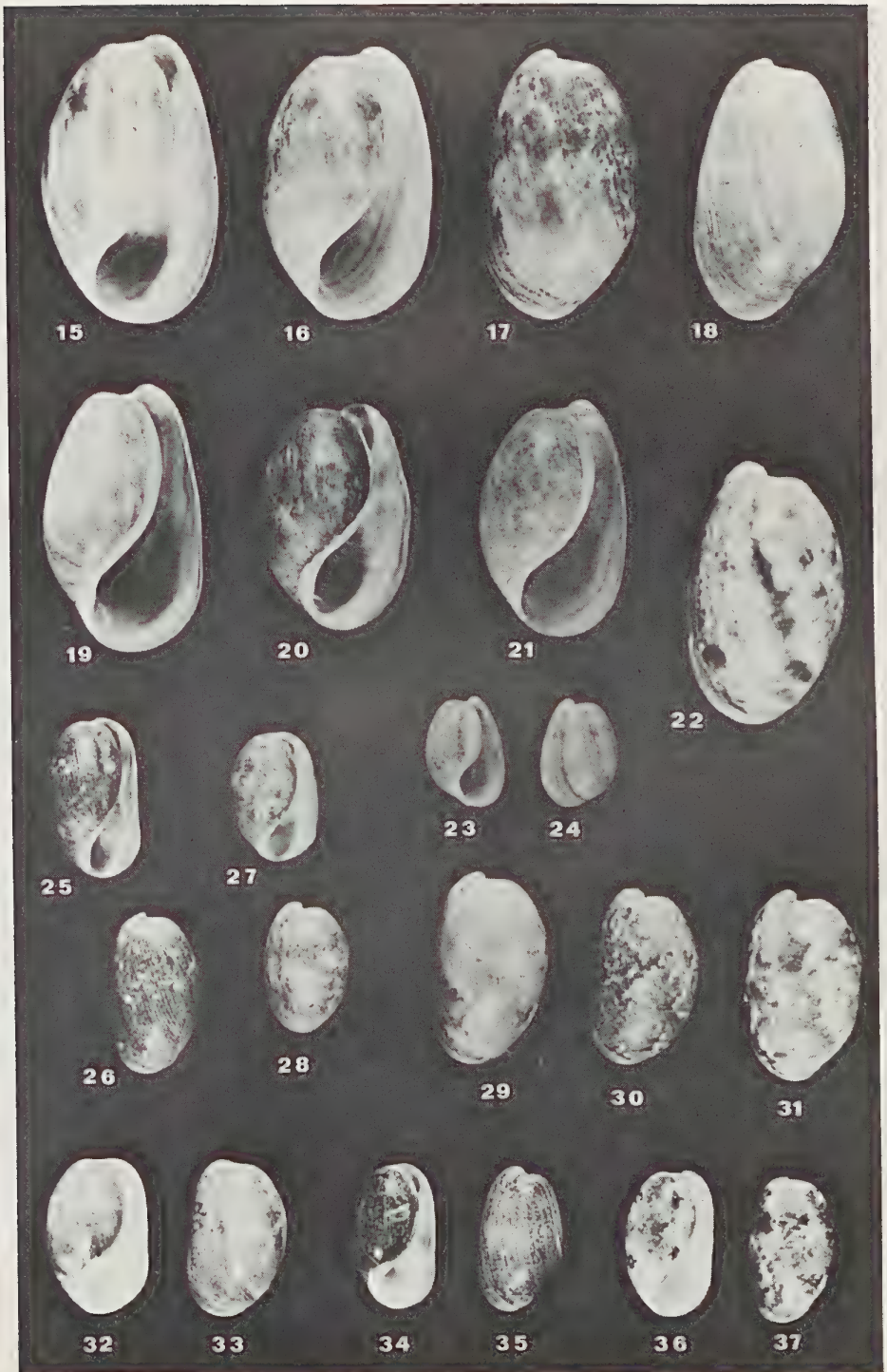
Details of anatomy have been given by Habe (1950) and Burn (1966). The author has examined the radulae of *B. vernicosa* from Lizard Island, North Queensland, and it is possible to reconcile the differences noted by Burn in respect to those of Habe in that the shape of the rachidian is dependent upon the orientation from which it is viewed; when observed flatly the rachidian has truncated sides; when tilted slightly forwards the sides of the rachidian appear to taper.

Live specimens observed at Lizard Island had light brown head shields and parapodia which were dappled with white, a darker band was present just in front of the eyes.

HABITAT: *Bulla vernicosa* is found throughout the tropical Pacific, frequently occurring sympatrically with *B. ampulla* Linnaeus and *B. punctulata* A. Adams in Sowerby. *B. vernicosa* inhabits lagoonal areas in the tropics, often in quite shallow water. Substrates in which it occurs range from clean coral rubble (e.g. Casuarina Bay, Lizard Island) to sand with a reasonable silt fraction (e.g. Erakor Lagoon, Port Vila, New Hebrides). Like *B. quoyii* and *B. angasi* it is nocturnal. I have found live specimens buried in fine sand beneath dead coral slabs during the daytime. Besides the nocturnal behaviour of the three *Bulla* species treated here, Abbott (1954) also noted that *B. occidentalis* A. Adams in Sowerby and *B. gouldiana* Pilsbry are to be found most abundantly at night and Robles (1975) both collected specimens of, and observed copulation in, *B. gouldiana* at night.

FIGURES 15-37.

15. *Bulla quoyii* Gray in Dieffenbach, The Grange, South Australia. 44.9 x 26.8 mm.
- 16, 17. *B. quoyii* Gray in Dieffenbach, Passage Island, southern side of Whangarei Harbour Entrance, New Zealand. 42.3 x 25.8 mm.
- 18, 19. *B. quoyii* Gray in Dieffenbach, elongate form, Mahurangi Heads West, North Auckland, New Zealand. 40.2 x 24.5 mm.
20. *B. quoyii* Gray in Dieffenbach, globose form, Bottle and Glass Rocks, Port Jackson, N.S.W. 30.2 x 24.1 mm.
21. *B. quoyii* Gray in Dieffenbach, Kohotutea Point, Cape Karikari, Northland, New Zealand. 35.6 x 22.0 mm.
22. *B. quoyii* Gray in Dieffenbach, Gunnamatta Bay, Port Hacking, N.S.W. 41.7 x 25.6 mm.
- 23, 24. *B. quoyii* Gray in Dieffenbach, adult of extremely globose form, Beach opposite Goat Island, Leigh, North Auckland, New Zealand. 16.1 x 11.8 mm.
- 25, 26. *B. angasi* Pilsbry, narrow form, Norfolk Island, 24.1 x 14.3 mm. (Hodge Coll., Zoology Department, University of Auckland).
- 27, 28. *B. angasi* Pilsbry, globose form, Rarawa Beach, Northland, New Zealand. 20.3 x 13.8 mm. (J. Coles Coll.).
- 29-31. *B. angasi* Pilsbry, colour variants, Norfolk Island. 29.1 x 18.7; 26.5 x 17.0; 29.3 x 19.0 mm respectively left to right.
- 32, 33. *B. angasi* Pilsbry, specimen with colouration matching lectotype, Rocky Bay, Tutukaka Harbour, Northland, New Zealand. 23.4 x 16.0 mm.
- 34, 35. *B. angasi* Pilsbry, Matapouri Beach, Northland, New Zealand. 22.3 x 13.4 mm.
- 36, 37. *B. angasi* Pilsbry, Amadée Island, New Caledonia. 22.7 x 14.5 mm.





Geographical distribution of *Bulla vernicosa* Gould (closed circles) and *B. angasi* Pilsbry (open circles). Map based only on localities from which specimens have been personally examined by the author. Map format courtesy of R. T. Abbott.

LOCALITY RECORDS: MAURITIUS: (AWBP). CHINA: Hainan Island (Guang-Yu & Si, 1965). JAPAN: (Habe, 1950; Kira, 1962). RYUKYU ISLANDS: Okinawa Island (AWBP; Hodge Coll.). CLEBES ISLANDS: Donggala (Adam & LeLoup, 1938). NEW GUINEA: Konori Island; Mioswoendi, Padaido Island (AIM); Manokwari (Adam & LeLoup, 1938). SOLOMON ISLANDS: Near Tulagi (AWBP). NEW HEBRIDES: Tanna Island, Erakor Lagoon and Mele Island, near Port Vila; Siviri Point, western end of Undine Bay (all Efate Island); Luganville foreshore and Tutuba Island (both Espiritu Santo Island) (all RCW). NEW CALEDONIA: Thio, Amadée Island off Noumea (both RCW). WESTERN AUSTRALIA: Broome (AIM); Roebourne (Hodge Coll.). QUEENSLAND: Nelly Bay, Magnetic Island; Casuarina Bay, western end of Lizard Island (AWBP); Rainbow Bay, Coolangatta; Capricorn Group (both Burn, 1966). FIJI: Pala'a Island (Hodge Coll.); Tevuki, Kandavu Island; North Coast, Viti Levu Island (both AIM); Manava Island (Cernohorsky, 1972). TONGA: (AWBP); Ma'apai Island (Hole Coll.). WESTERN SAMOA: (Hodge Coll.): Beach 20 miles from Apia (Hole Coll.); Pilot Point, Apia (AWBP); Moatoa Beach; Apia Harbour (both AIM). COOK ISLANDS: (AIM). RAROTONGA ISLAND: (Hodge Coll.).

DISCUSSION: *Bulla vernicosa* Gould is a distinctive tropical species because of its globose shape, relatively constant colour pattern and large apical cavity. It appears to be most closely related to *Bulla ampulla* Linnaeus. A careful comparison with the more temperate *B. angasi* shows several features to differ consistently in the two species. *B. vernicosa* is larger, its shell is globose with greatest width near the middle; the outer lip is evenly convex; the apical cavity is open and perspective; there is a narrow but open umbilical chink where the reflected umbilical callus does not quite rejoin the shell, this chink is most noticeable in juvenile shells; in the mouth the thickened ridge extends the whole length of the outer lip; colouration is relatively consistent and a "punctulate" pattern is never exhibited. *B. angasi* is smaller, the shell is constricted medially so that greatest width is near the base, the upper part of the aperture is narrow; the apical cavity is small with spire whorls hardly visible; frequently the umbilical callus is reflected completely back to the shell leaving no umbilical chink; the thickened ridge extends only to the medial constriction of the outer lip; colour patterns in any given population are variable and this species may exhibit a "punctulate" pattern.

ABBREVIATIONS USED IN TEXT

- AIM. Molluscan Collection, Auckland Institute and Museum.
- AWBP. A.W.B. Powell Collection, Auckland Institute and Museum.
- RCW. R.C. Willan Collection, Auckland.
- SEM. Scanning Electron Microscope.

ACKNOWLEDGEMENTS

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A NEW GENERIC PLACEMENT FOR *SCABRICOLA BACKAE* CERNOHORSKY, 1973.

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SUMMARY

Scabricola backae is transferred to the genus *Mitra* on the basis of radular morphology.

REMARKS

Developing a reasonable system of taxonomy for the family Mitridae has been a difficult problem that has been aided substantially by the work of Cernohorsky (1966; 1976). Cernohorsky (1966) remarked that a generic placement of mitre species based on shell morphology alone was insufficient. The shells of some genera are very similar but the radular morphology may be quite different. Accordingly the generic arrangement Cernohorsky proposed was based primarily on the structure of the radula. Only tentative placements could be made for species where the shells were known but no radulae were available for examination. As radulae were subsequently found the initial generic placement would be substantiated or could prove erroneous. Just such an erroneous placement has recently been encountered.

Cernohorsky (1973) described a new species, *Scabricola backae*, from Flinders Bay, Augusta, Western Australia (Figure 1). The localities at which the holotype and nine paratypes were collected showed the species to have a range from the cool, temperate waters of Augusta northwards to the tropical waters at Onslow. No radula was available when *S. backae* was described and the species was placed in the genus *Scabricola* on the basis of shell morphology.

The radula of *Scabricola variegata* (Gmelin, 1791), the type species of the genus, was figured by Cernohorsky (1976). The central tooth has eight cusps that are largest in the medial portion of the tooth (Figure 2A). The lateral teeth have four cusps medially, and none on the leading edge of the tooth. The radula of *Mitra mitra* Linnaeus, 1758, the type species of the genus *Mitra*, has a central tooth with five cusps (Figure 2B). The lateral teeth have numerous cusps which are large medially and taper off in height distally.

The radula was removed from a live collected specimen of *Scabricola backae* found at Augusta, Western Australia, in January 1977 by Mrs. Wendy Anson (WAM 47-77). The radula (Figure 2C) had 56 rows of teeth; each row consisted of a central tooth flanked on each side by a single lateral tooth. Comparison of the radula of *Scabricola backae* with those of *Mitra mitra* and *Scabricola variegata* demonstrates a close affinity of *S. backae* with *M. mitra* and no relationship with *S. variegata*. *Scabricola backae* should thus be transferred to the genus *Mitra*.

ACKNOWLEDGEMENTS

Mrs. Glad Hansen brought the question of the generic status of *Scabricola backae* to my attention. She and Mrs. Wendy Anson made a special trip to Augusta to collect a live individual from which a radula could be obtained.



Figure 1.
The holotype of *Scabricola backae* (WAM 14-72), shell height 22 mm.

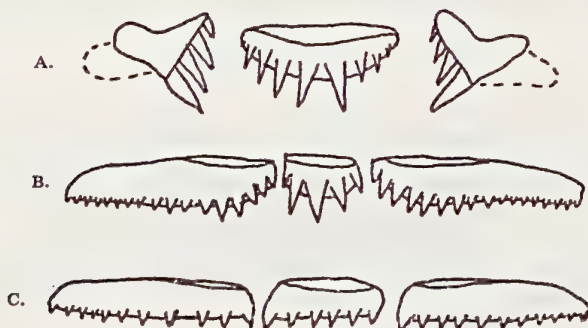


Figure 2.
A row of radular teeth of *Scabricola variegata* (A) and *Mitra mitra* (B) (after Cernohorsky, 1976), and *Scabricola backae* (C).

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NOTES ON THE DISTRIBUTION OF SEX AND SHELL CHARACTERS IN SOME AUSTRALIAN POPULATIONS OF *POTAMOPYRGUS* (GASTROPODA : HYDROBIIDAE)

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SUMMARY

Figures are presented for the proportions of the sexes and shell types in collections of the fresh water prosobranch *Potamopyrgus* from areas of Australia. Findings are compared with those from populations in New Zealand.

N.B. Representative material from these collections has been deposited in the Australian Museum, Sydney, and from the Victorian localities, also in the National Museum of Victoria, Melbourne.

INTRODUCTION

Snails of the hydrobiid genus *Potamopyrgus* have long been renowned (under sundry names) for their remarkable variability (e.g. Pettard 1888) and since the early decades of this century it has been known that many of them reproduce parthenogenetically (for review and references - Winterbourn 1970 a & b). Such peculiarities make these animals extremely interesting from the standpoint of population genetics - but at the same time it is understandable that some uncertainty surrounds the status of the species in the genus.

Populations of *Potamopyrgus* which are ovo-viviparous, and generally seem capable of reproducing parthenogenetically, are found in Australia, New Zealand and Europe under the names of *P. nigra* (Ouoy & Gaimard), *P. antipodum* (or *antipodarum*) (Gray) and *P. jenkinsi* (Smith) respectively. The question of the identity or otherwise of these three named species (or for that matter the possibility of their further subdivision) will not be discussed here and the generic name will be used on its own to refer to any of these three. No reference will be made to any oviparous members of the genus.

Investigations into the genetics of these snails and the make up of their populations in New Zealand has led to an interest in the basis (genetic, environmental or both) of the widely differing sex ratios found in natural populations. At the same time the occurrence of periostracal spines or other shell "decoration" continues to present unsolved problems.

Field studies in New Zealand have involved sampling populations from a number of different localities and scoring for sex and shell decoration. Some of these populations

have been repeatedly sampled over a number of years. The percentages of males in these collections have ranged from 0-50 and of decorated shells, from 0-100. Furthermore, under repeated sampling, contrasting populations have maintained their distinction in both respects over more than five years.

During this work a period of leave has been spent in Australia to make some comparisons of populations in the two countries.

METHODS

At each locality, living snails are collected by any convenient means and a sample - generally about 100 and never less than 30 - is examined under a 10X stereomicroscope and the animals sorted according to sex and shell decoration.

Sex is established by holding each snail upside-down under water until its movements give a clear view of the right side of the neck; males being recognised by the penis. To avoid mistakenly classing undeveloped males as females, a lower size limit is imposed. Sorting is done over 1 mm graph paper to allow an approximate estimate of shell length, and individuals of less than 2.5 mm are not scored unless recognisable males below this size are present. In populations of large mature size, this lower limit is raised. Above the limit chosen, any snail without a visible penis is regarded as female - no evidence of adult aphaallic males being known.

Shell decoration is taken to include anything from the finest line down some or all of the whorls to a series of conspicuous spines. Shells on which no such feature is visible are classed as smooth.

RESULTS

Two sets of collections were made in main-land Australia, one around Sydney, the other in the neighbourhood of Melbourne and Geelong. One sample was received from Tasmania.

Maps 1 & 2 indicate by number the localities at which *Potamopyrgus* was found in each mainland district. Counts and percentages obtained are set out, under corresponding numbers, in Table 1.

Size was not recorded in detail but it was noted that the shell length of the main group of mature snails never exceeded 4.45 mm; and in some populations was considerably smaller.

DISCUSSION

Although the information presented here is so limited that further collections may alter the picture considerably, it may still be worth making a few comparisons.

1. Size - The Australian snails are over-all, decidedly smaller than their New Zealand counterparts, though well within the lower range of these.
2. Decoration - The ranges in frequency of decorated shells are much the same in the two countries, and in both the Australian regions, though it was surprising to find no wholly smooth samples among the collections from Victoria.
3. Sex - Males are particularly scarce in the New South Wales collections, having been found only in one of the 28 localities. Even there they only formed about 0.25% of the population. In Victoria males were more abundant, occurring in 5 out of 11 collections and reaching 9% in one. By New Zealand standards however, even this is low.

Direct comparison with equivalent New Zealand figures is difficult as the work there has mainly involved repeated sampling from a restricted number of populations, rather than a general survey. However, by taking only the most recent count for any locality sampled more than once, figures for 73 stations can be assembled for comparison. Table 2 shows the number of these collections which fell into each level of male frequency. It is evident that not only were males found in a greater proportion of the New Zealand collections than in the Australian, but that they commonly formed a much larger percentage of the population.

In this connection it is interesting to recall that in Europe - where *Potamopyrgus* has been spreading since the 1880's, males are a great rarity (Patil 1958).

Dr. W.F. Ponder suggests (personal communication) that the largely female population of the Sydney area could, in a similar way, be associated with recent immigration, for the collections of the Australian Museum contain no specimens of this snail from New South Wales before 1960.



Map 1. New South Wales survey area



Map 2. Victoria survey area

TABLE 1
Data on sex and shell decoration in *Potomopyrgus* from some Australian localities.
(D - decorated shell, S - smooth shell)

No.	Locality	Date Collected	Total	SAMPLE COUNTED				% Males	% D	Shells or preserved material available†
				Males		Females				
				D	S	D	S			
NEW SOUTH WALES (Map 1)										
1	Cattai creek	6/3/75	100	—	—	—	100	0	0	
2	Thornleigh gully 1.	5/3	112	—	—	—	112	0	0	
3	Thornleigh gully 2.	5/3	103	—	—	—	103	0	0	
4	Spring gully	5/3	102	—	—	—	102	0	0	
5	Cowan's creek	5/3	100	—	—	—	100	0	0	
6	Kurin-gai creek 1.	4/3	102	—	—	5	97	0	5	†
7	Kurin-gai creek 2.	9/2	100	—	—	—	100	0	0	
8a	Never fail creek	9/2	82	—	—	17	65	0	23	†
8b	Never fail creek	4/3	115	—	—	59	66	0	51	†
9	Narrabeen creek	4/3	121	—	—	—	121	0	0	†
10	Quarry branch	6/3	101	—	—	—	101	0	0	
11	Vineyard creek	5/3	120	—	—	1	119	0	1	
12	Devlin's creek	5/3	46	—	—	13	33	0	28	
13	Terry's creek	5/3	102	—	—	—	102	0	0	
14	Shrimpton's creek	5/3	88	—	—	—	88	0	0	
15	De Burgh creek	5/3	119	—	—	62	57	0	52	
16	Un-named creek	5/3	100	—	—	97	3	0	97	
17	Stony creek	4/3	78	—	—	—	78	0	0	
18	Rocky creek	5/3	101	—	—	—	101	0	0	
19	Gordon creek	5/3	83	—	—	—	83	0	0	
20	Oxford creek	15/2	121	—	—	—	121	0	0	
21	Middle creek	15/2	200	—	—	—	200	0	0	
22	Middle creek	2, 15/2	119	—	—	—	119	0	0	
23	Middle creek	3, 27/2	104	—	—	—	104	0	0	
24a	Middle creek	4, 15/2	603*	—	1	77	525	(1)	18	†
24b	Middle creek	4, 27/2	255	—	1	32	222	(1)	12	
25	Middle creek	5, 27/2	101	—	—	6	95	0	6	
26	Middle creek	6, 27/2	32	—	—	—	26	0	20	
27a	Middle creek	7, 15/2	262	—	—	253	9	0	95	†
27b	Middle creek	7, 27/2	91	—	—	78	13	0	86	†
28	Little Willandra creek	4/3	119	—	—	10	109	0	9	
										* extra numbers counted after finding male.

* extra numbers counted after finding male.

VICTORIA (Map 2)										
1	Stony creek	11/3	117	1	—	69	47	1	60	†
2	Spout creek	11/3	120	9	—	101	10	9	92	†
3	Wauru Ponds	11/3	100	—	—	2	98	0	2	†
4	Barwon river	11/3	178	4	—	120	54	2	70	†
5	Hovell's creek	1. 11/3	169	—	—	65	104	0	38	†
6	Hovell's creek	2. 14/3	58	—	—	12	46	0	21	†
7	Hovell's creek	3. 14/3	33	—	—	8	25	0	24	†
8	Hovell's creek	4. 14/3	61	—	—	1	60	0	1	†
9	Werribee river	14/3	136	2	3	63	68	4	45	†
10	Skeleton creek	14/3	52	—	—	5	47	0	10	†
11	Kororoit creek	14/3	167	—	6	1	160	4	(1)	†
TASMANIA										
1	"Muddy creek" W. Side of Tamar estuary (41°20'S, 147°03'E)	19/4	154	—	—	22	132	0	14	

TABLE 2
Percentage of males in a range of New Zealand collections of *Potamopyrgus*

Percentage of males	0	1-9	10-19	20-29	30-39	40-50	Total
No. of collections represented	23	15	5	12	12	6	73

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I am particularly grateful to W.F. Ponder for facilities and help during leave spent at the Australian Museum, Sydney. I also want to thank B.J. Smith for a week at the National Museum, Melbourne; also R. Burn for guidance in the field; Mr. & Mrs. N. Ireland and N. Campbell for collecting expeditions and the latter also for a number of samples from the Sydney area. I am grateful to R.C. Kershaw for the collection from Tasmania.

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FURTHER NOTES ON THE CLAVAGELLIDAE, WITH SPECULATION ON THE PROCESS OF TUBE GROWTH

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INTRODUCTION

Following the publication of revisionary work on the family Clavagellidae (Smith 1971, 1976), an opportunity was taken to examine collections and libraries in several European museums. In the Museum d'Histoire Naturelle, Paris, several important specimens were discovered, including a hitherto unrecognised Lamarck type, and two important papers, previously overlooked, were brought to my notice.

REMARKS

In the revision of the Australian clavagellids (Smith, 1971), *Aspergillum agglutinans* Lamarck, 1818 was placed in the synonymy of *Brechites* (*Foegia*) *novaezelandiae* (Bruguiere, 1789). It was stated that no type specimen of *A. agglutinans* could be found in the Paris or Geneva Museums. Two syntypes of *A. novaehollandiae* Chenu, 1843 where the only types of any of the synonyms of *B. (F.) novaezelandiae* which could be found at that time. On a recent trip to Paris I discovered a specimen of *A. agglutinans* which, after examination of the labels and comparison with figures, was identified as the type of that species. The specimen was broken and a drawing of the anterior part showing the position of the valves and tubules, drawn from a colour transparency of the specimen, is given here. The type locality is given as New Holland and the collectors as Peron and Lesueur, 1801. This specimen confirms the placement of this species in the synonymy of *B. (F.) novaezelandiae*, since the valves are partially covered by swollen prominences and the tubules of the anterior end are not arranged into a disc with a distinct fringe. Width of the swollen anterior end at its widest point is 13 mm.

Several specimens in the collections in Paris carried unfamiliar names attributed to Jousseaume. With the valuable assistance of M. Tillier of that institution, two papers overlooked in the earlier work were brought to my notice. These were one by Jousseaume (1888) in which he erected the name *Clavagella adenensis* for clavagellid specimens from Aden and Djibouti in the Red Sea and one by Lamy (1923) based on manuscript notes of Jousseaume, redescribing the above species and describing three other Jousseaume manuscript names, *Briopa socialis*, *Bryopa senilis* and *Bryopa astraicicola*. Lamy attributed all four species to Jousseaume indicating by quotation marks that the descriptions and other information were transcribed direct from manuscript notes of Dr. Jousseaume. Because the name *Clavagella adenensis* was proposed without an adequate description (Jousseaume, 1888) it is here considered a *nomen nudum*. It was first properly proposed and described in Lamy (1923) under the name *Bryopa adenensis*. In that work Lamy makes it clear that the descriptions and names should be attributed to Jousseaume, so these four species of *Bryopa* should be cited as Jousseaume in Lamy 1923.

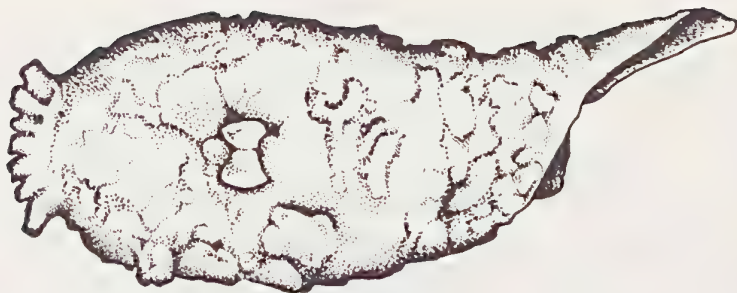


Figure 1. Holotype of *Aspergillum agglutinans* Lamarck, 1818 (= *Brechites* (*Foegia*) *novaezealandiae* (Bruguiere, 1789)).

In this paper Lamy suggests that the four species are so similar that the characters used in their separation could be attributed to individual variation brought about by the accidental circumstances of the habitat. Several specimens labelled *Clavagella adenensis* and *Clavagella socialis* from both Aden and Djibouti were found in the Jousseume collection, including specimens which were probably the types. These four species are here considered synonyms of *Clavagella* (*Bryopa*) *aperta aperta* (Sowerby, 1823) since they are clavagellids with one free valve, embedded in chambers in limestone and coral, with large valves, an oval to figure-8 section tube and reflected tube ends. The presence of these specimens in the southern Red Sea confirms the records of Soliman (1971) and necessitates the extending of the range of this species to the junction of the Red Sea and the Indian Ocean.

Lamy also reproduced some notes by Jousseume on the early development and way of life of the large common Red Sea clavagellid *Brechites* (*Brechites*) *vaginiferus vaginiferus* (Lamarck, 1818). Jousseume speculated that this species commenced life as an ordinary bivalve with a planktonic larval stage before settling to take up the sedentary habit. From field observations, he described how the animal orientates itself perpendicularly in the sand with the open end of the tube protruding from the sand. The animal then draws water in through its protruded siphon and filter feeds like most other bivalves.

This paper, together with other work on this interesting family, leads me to speculate on the mechanism of tube development in the Clavagellidae. The tubes of these animals always have foreign bodies such as sand grains, stones and shells incorporated into their structure. However this foreign material is never attached to the valves. No growth discontinuities are seen along the length of the tubes, though in some specimens, tube repair and addition of length as extra plaited ruffles can occur. The other salient fact is that although a reasonable accumulation of specimens is available for study in the world's museum collections, in none of the major collections I have examined could I find what appeared to be a juvenile tube. From these facts the inference can be drawn that the valves and the tube are secreted at different times; that the valves are not in contact with the substratum when they are secreted; that the tube substance is in direct contact with the substratum when it is secreted and that the animal only secretes one tube in its life and that tube must be secreted as an adult-sized tube with the only possibility for growth being in length at the open end, but nowhere else. From this point it is therefore possible to put forward speculation on the processes that clavagellids might undergo to form the tube.

The juvenile clavagellids, after hatching, probably spend some time in the plankton with a normal bivalve shell as other bivalves. On settling they continue to grow until the body is much larger than the small bivalve shells. This "slug" stage may last for some considerable time. They then burrow into the substratum, orientate to a vertical position and expand their body by muscular and hydrostatic means into the adult tube size. They then secrete a calcareous shell-substance from all over their mantles to form the tube. This shell-substance, before it has hardened, picks up particles from the substrate. No similar mechanism of shell production is known for any other

bivalve, but in its essentials, this is the process that most nearly accounts for all the salient observations of this unusual family.

ACKNOWLEDGEMENTS

I would like to thank M. Simon Tiller of the Malacologie Department of the Museum National d'Histoire Naturelle, Paris for his kindness and great assistance in locating the material and literature on which this work is based. Thanks are also expressed to Ms. Rhyllis Plant for drawing the specimen and Mrs. Lyn Anderson for typing the manuscript. Thanks are due to the Science and Industry Endowment Fund, to Comalco (Australia) Pty. Ltd., to B.H.P. Ltd. and to the Council of the National Museum of Victoria for financial assistance to enable me to visit museums in Europe.

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ON THE TAXONOMIC STATUS OF THE GENERA *ACUTOPLAX* COTTON & WEEDING, 1939 AND *EUDOXOPLAX* IREDALE & MAY, 1916 (MOLLUSCA: POLYPLACOPHORA)

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SUMMARY

The genera *Acutoplax* Cotton & Weeding, 1939 and *Eudoxoplax* Iredale & May, 1916, both recently considered as synonyms of *Callochiton* Gray, 1847, are reviewed. The taxonomic limits of *Acutoplax* are changed, and it is concluded that *Acutoplax* and *Eudoxoplax* are valid subgenera of respectively *Callochiton* Gray, 1847 and *Eudoxochiton* Shuttleworth, 1853.

INTRODUCTION

The study of a good specimen of *Callochiton mayi* Torr, 1912, graciously given to me by Mr. J.R. Penprase, has revealed a peculiar feature which, upon further investigation in the collection of the Tasmanian Museum and in his private collection by Mr. Penprase, has proved to be of special taxonomic interest. Advantage is taken of this note to reconsider the status of *Eudoxoplax* Iredale & May, 1916.

TAXONOMY

Acutoplax Cotton & Weeding, 1939

The genus *Acutoplax* was created with the following diagnosis: "Shell small to medium, elongate oval, elevated and carinated. Sculptured with longitudinal sulci on the pleural areas. Girdle of packed spicules. Well developed insertion plates with grooved teeth. End and median valves multi-slit. Genotype: *Callochiton mayi* Torr, 1912" (Cotton & Weeding, 1939: 189).

If this diagnosis is compared with the original description of the genus *Callochiton*: "The valves keeled, the hinder valve entire; the plates of insertion rather short, thick, of the terminal valves divided into many, and of the central valves into four bifid lobes. Margin with imbricate scales. ^o Margin with lanceolate, elongate, erect, closely-pressed scales. *Chiton laevis*, Montagu" (Gray, 1847: 126), it seems logical that *Acutoplax* should be considered a synonym of *Callochiton*. Especially if one knows that the type-species of the genus *Callochiton*, *Chiton laevis* Montagu, 1803 (pre-occupied by *Chiton laevis* Pennant, 1777 = *Tonicella rubra* (Linnaeus, 1767)) = *Chiton achatinus* Brown, 1827 exists in two forms: the typical Atlantic Ocean form without any sulci on the pleural areas, and the Mediterranean Sea form *doriae* Capellini, 1859, with up to five longitudinal sulci on the pleural areas.

In the description of *Callochiton mayi*, Torr (1912: 1) says about the girdle: "Densely covered with microscopically diamond-shaped scales, which are only the points of long flattened, closely

appressed corneous bodies. This helps to fix the genus of this shell". Indeed, this description fits the girdle of *Callochiton achatinus* extremely well, and not only of the type-species, but of all other *Callochiton* species. Since then, as far as I know, no further study has been made of the rare North Tasmanian species *Callochiton mayi* Torr, 1912.

A.G. Smith (1960: I 58) accepts only two valid genera in the family *Callochitonidae*: *Callochiton* Gray, 1847 and *Eudoxochiton* Shuttleworth, 1853. All other related taxa are considered synonyms of *Callochiton*. They are: *Clathropleura* Tiberi, 1877 (partim); *Trachyradsia* Carpenter in Dall, 1878; *Collochiton* Sars, 1878 (nom. null.); *Stereochiton* Carpenter in Dall, 1882; *Icoplax* Thiele, 1893; *Eudoxoplax* Iredale & May, 1916; *Paricoplax*, *Quaestiplax* Iredale & Hull, 1929; *Acutoplax* Cotton & Weeding, 1939 and *Ocellochiton* Ashby, 1939.

In April 1976, my good Tasmanian friend Mr. J.R. Penprase sent me a specimen of *Callochiton mayi* Torr, 1912. He had collected the specimen on March 22nd 1976 at the western end of Coles Beach, West Devonport, north coast of Tasmania, at the bottom of a stone lightly embedded in sand in hipdeep water at low tide. The specimen was preserved in an alcohol-solution.

While studying the specimen, I noticed that the girdle showed the typical covering of any *Callochiton*, but besides that it had many bunches of 2-4 very long and slender corneous processes standing quite erect at about 1/3 from the outside border of the girdle.

This very peculiar feature incited me to check the literature again, but nowhere could I find any notice of it. At my request Mr. Penprase examined the *Callochiton mayi* specimens in his own collection and those in the collection of the Tasmanian Museum for this feature. In a letter dated 27 March 1977, he let me know that all the spirit specimens he had studied had the corneous processes on the girdle. About the holotype (Tasmanian Museum Reg. No. E177a/7518a) he wrote: "The Type specimen is dry, glued to cardboard, about half the girdle folded under and not accessible. No corneous processes can be seen under the microscope (100 x). In view of the rather battered state of the Type it could well have had such a fragile feature inadvertently wiped off before Torr got around to writing the description".

From all this, I think we may safely conclude that *Callochiton mayi* should no longer be considered as belonging to *Callochiton* s.s. The characteristics of the girdle are so different that a subgeneric distinction must be made. A new subgeneric name might be proposed, but I think another solution is possible. Article 61 of the International Code of Zoological Nomenclature (1964: 59) about the relationship of the type to the taxon, says: "The 'type' affords the standard of reference that determines the application of a scientific name. Nucleus of a taxon and foundation of its name, the type is objective and does not change, whereas the limits of the taxon are subjective and liable to change . . .". As *Callochiton mayi* is the type of the genus *Acutoplax* Cotton & Weeding by original designation, I propose to maintain that name, with subgeneric value, and to emend the diagnosis in the following sense: Girdle of packed spicules and interspersed bunches of several long corneous processes.

Other species that have been assigned to the genus *Acutoplax* are: *Callochiton rufus* Ashby, 1900; *Callochiton klemi* Ashby, 1926 and *Acutoplax cottoni* Weeding, 1940. All these species have the characteristic *Callochiton* girdle, but none have the supplementary bunches of corneous processes, so they all belong to the genus *Callochiton* s.s.

It seems probable that the subgenus *Acutoplax* Cotton & Weeding, 1939 consists of one species only: *Callochiton (Acutoplax) mayi* Torr, 1912.

Eudoxoplax Iredale & May, 1916

The genus *Eudoxoplax* was proposed for *Chiton inornatus* Tenison-Woods, 1881. From the original diagnosis I quote: "Recent acquisitions of many specimens show the Tasmanian shells to reach a large size, and to differ appreciably from *Callochiton* and approach very closely to *Eudoxochiton*. It differs from the latter in the very wide leathery girdle with very short thin curved few and minute little hairs, and may later be regarded as a subgenus of *Eudoxochiton*" (Iredale & May, 1916: 99).

Indeed, *Chiton inornatus* has very little in common with the type or other members of the genus *Callochiton*. It leans very close to the genus *Eudoxochiton* Shuttleworth, 1853, type-species *Acanthopleura nobilis* Gray, 1843. Only the girdle-elements differ markedly. The "very short thin curved few and minute little hairs" of *Chiton inornatus*, are replaced in *Eudoxochiton* by many

scattered rigid spinelets. Why *Eudoxoplax* has been synonymized with *Callochiton* rather than with *Eudoxochiton* is an open question. As Iredale & May suggested, *Eudoxoplax* should be considered a subgenus of *Eudoxochiton*, the differences of the girdle-elements having too little value to make a generic distinction.

As a result of the above observations, the subfamily *Callochitoninae* should be divided as follows:
Subfamily *Callochitoninae*

Genus *Callochiton* Gray, 1847 (Type: *C. achatinus* (Brown, 1827))

Subgenus *Callochiton* s.s.

Subgenus *Acutoplax* Cotton & Weeding, 1939 (Type: *C. (A.) mayi* Torr, 1912)

Genus *Eudoxochiton* Shuttleworth, 1853 (Type: *E. nobilis* (Gray, 1843))

Subgenus *Eudoxochiton* s.s.

Subgenus *Eudoxoplax* Iredale & May, 1916 (Type: *E. (E.) inornatus* (Tenison-Woods, 1881))

ACKNOWLEDGEMENTS

I wish to thank Mr. J.R. Penprase for the preserved specimen of *Callochiton mayi* and for examining other material of this species in the Tasmanian Museum and his private collection, and the staff of the Tasmanian Museum for allowing him to do so on my behalf.

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EGG CAPSULES AND EARLY DEVELOPMENT IN *SIPHONARIA DIEMENENSIS* (QUOY & GAIMARD, 1833) AND *SIPHONARIA BACONI* (REEVE, 1856).

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SUMMARY

Spawn of two species of the littoral pulmonate genus *Siphonaria* from Victoria are described and found to differ only in a few minor features. Development of the two species is also similar and is followed from egg-laying to hatching of a free swimming veliger phase. *S.diemenensis* is in general more vigorous and develops more rapidly than *S.baconi* under the same conditions. Measurements of embryos and capsules at different developmental stages show that while the embryo increases in overall size from egg to hatching, the capsule size does not alter significantly during this period.

INTRODUCTION

Molluscs of the marine pulmonate gastropod genus *Siphonaria* are common members of communities on Victorian rocky shores. *S.diemenensis* occurs throughout the littoral zone on open rock platforms and, to a lesser extent, on sheltered rocks. *S.baconi* has a more restricted distribution, but is also found on open rock platforms in association with *S.diemenensis* (Macpherson & Gabriel, 1962).

The eggs, spawn and early development of a number of littoral gastropods has been described for the Sydney area by Anderson (1960, 1961, 1962, 1966) and for the Melbourne area by Murray (1962, 1966, 1969, 1970) and Black (1976), but these do not include marine pulmonates. The only work of this type on *Siphonaria* is for *S.pectinata* from Florida (Voss, 1959). The aim of the present work is to describe the spawn and follow the early development within the capsule through to hatching; a later extension is planned to study the growth of the veliger from hatching to metamorphosis.

MATERIALS AND METHODS

Spawn from *S.diemenensis* and *S.baconi* was collected from a sandstone reef at Portsea, Victoria during the summer of 1975 - 6. Individual egg masses were measured and kept in litre beakers

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containing glass filtered seawater (pore size $3\mu\text{m}$), which was changed weekly, and covered with polythene to reduce bacterial contamination. Adults of each species were also collected and placed in a tidal tank system at La Trobe University; spawn was produced and its subsequent development followed in the tank. All spawn was maintained at 15°C , and a daily sample examined under the microscope. Photographs were taken using an Olympus PM-6 camera mounted on a GB microscope.

DESCRIPTION OF SPAWN

Siphonaria diemenensis

The eggs are laid as a ribbon in a collar or spiral-shaped mass usually almost circular in outline (Fig.1A). Mean dimensions are given in Table 1. Each egg is contained in a capsule and the capsules are connected by threads (Fig.2). The network of capsules is embedded in a fairly turgid clear jelly surrounded by a clear protective covering layer 0.34mm thick. The colour of the spawn varied with stage of development, from a pale or mid-yellow colour at the time of deposition to the mid-veliger stage, and a darker golden yellow from late mid-veliger stage to hatching.

TABLE 1 : Mean dimensions of the egg masses of two *Siphonaria* species. (S.D. - standard deviation)

	<i>S. diemenensis</i>		<i>S. baconi</i>	
Max. dimensions	10.31 x 11.26		9.19 x 7.80	
mm	(S.D.2.5)	(S.D.2.7)	(S.D.6.7)	(S.D.5.2)
Ribbon width	1.19		2.83	
mm	(S.D.1.1)		(S.D.0.4)	
Ribbon height	5.31		1.64	
mm	(S.D.2.0)		(S.D.0.9)	

Siphonaria baconi

The eggs are also laid as a ribbon (Fig.1C), which is again usually collar shaped (although never a spiral), but frequently irregular in outline; occasionally a very wide open collar is laid, or a long irregular trailing ribbon. The collars are without exception much flatter than those of *S.diemenensis*. Mean dimensions are given in Table 1. The capsules each contain one egg and are similar in shape and size to those of *S.diemenensis*, but the jelly is less turgid and its clear covering varies in thickness from 0.18mm at the sides to negligible thickness on top. Sand grains, diatoms and other debris characteristically adhere to the jelly masses from Portsea, although were not available for adherence to masses laid in the tidal tanks. The spawn colour differs from *S.diemenensis*, varying from pale cream to white at deposition to trochophore stage, cream at trochophore to mid-veliger and dark cream in the advanced veliger stage to hatching.

Spawning time

Initial limited observations suggest that new spawn is only deposited by *S.diemenensis* during spring tides. The periods when spawn was laid in laboratory tanks also coincided only with spring tides. In contrast, newly deposited spawn of *S.baconi* was collected on the shore and laid in laboratory tanks only during neap tides. However, these preliminary observations require further verification in the field.

EARLY DEVELOPMENT

Siphonaria diemenensis

Egg masses spawned in captivity and maintained in tidal tanks at 15°C reached hatching stage in 7 to 10 days. Hatching was determined as the date when the first free swimming veliger larvae were released. These limits may be more variable in the natural habitat where masses are exposed to greater fluctuations in environmental conditions.

A series of developmental stages is described below and illustrated in Fig.3 A to I. Maximum dimension of early stages and maximum shell length of later stages are given in Table 2. Cleavage

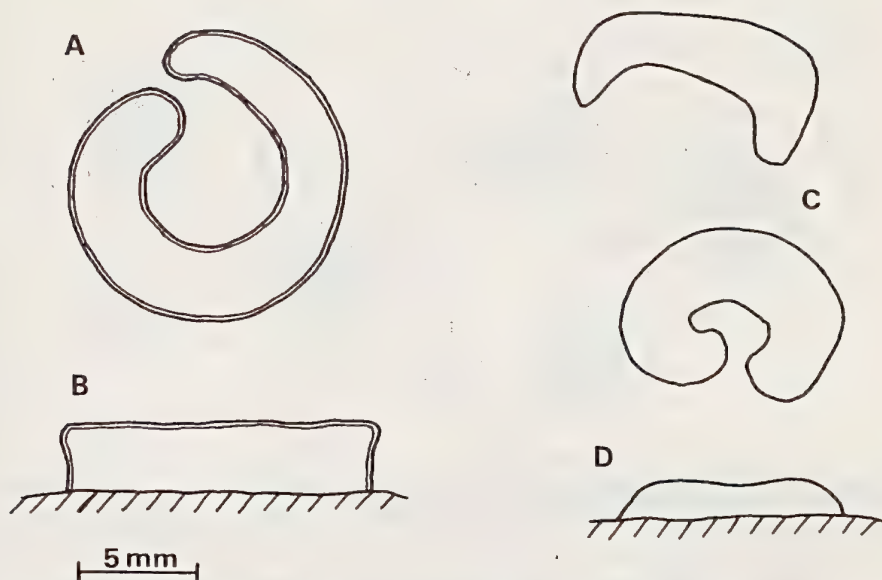


FIGURE 1. A, *S. diemenensis* : View from above of typical egg mass. B, *S. diemenensis* : Lateral view of egg mass attached to substrate; capsules are embedded in a turgid jelly with a distinct clear layer over the surface of the mass. C, *S. baconi* : View from above of two egg masses: there is more variation in shape in this species. D, *S. baconi* : Lateral view of egg mass attached to substrate; capsules are embedded in a less turgid jelly than *S. diemenensis* and there is no distinct clear layer over the surface of the mass.

occurs rapidly once the eggs are laid and within 24 hours a placula blastula of large distinct cells is formed (Fig. 3 A,B,C). Macromere diameter decreases from $50\mu\text{m}$ in the 2-cell stage to $29\mu\text{m}$ in the early blastula stage but thereafter cells were too small for accurate measurements. These cells further subdivide during the next 24 hours. One surface of the blastula becomes concave (Fig. 1 E) and in the centre of this area cells move into a slit-like blastopore as gastrulation occurs (Fig. 1 D). Large yolky macromeres are visible inside the early blastula, but become obscured by the time gastrulation is completed 2 days after laying. During the third day a band of very small cilia develop (length $4\mu\text{m}$) and the embryo, still gastrula-shaped but now termed a trochophore, begins to move slowly (Fig. 1 E). Polar bodies extruded during early cleavage remain visible up to the trochophore stage in some specimens.

During the fourth day a thin triangular shell rudiment (max. length $73\mu\text{m}$) develops enclosing undifferentiated tissue (including much yolk) which forms the visceral hump. Velar lobes start to grow out and the cilia (length $10\mu\text{m}$) enlarge to form the velum. The foot begins to develop as a short square outgrowth beneath the velum and a very thin operculum becomes visible on its posterior surface. This is the early veliger stage (Fig. 1 G). Much growth of shell, velum and foot and differentiation of internal organs occurs over the next 3 to 4 days to form ultimately the advanced veliger stage which is ready to hatch. By the mid-veliger stage (Fig. 1 H) a pair of prominent statocysts have formed and the stomach and digestive gland are distinct. The larval heart has begun to beat spasmodically. Cilia have formed over the surface of the foot, and the operculum now projects beyond the foot edge. Torsion occurs and can be easily recognized by the appearance of the rectum in a dorsal position above the velum, with the anus opening into the left side of the mantle cavity. Shell growth continues asymmetrically due to torsion and the thickened glandular mantle edge is attached to the shell rim. By the seventh to tenth day after laying torsion is complete and the

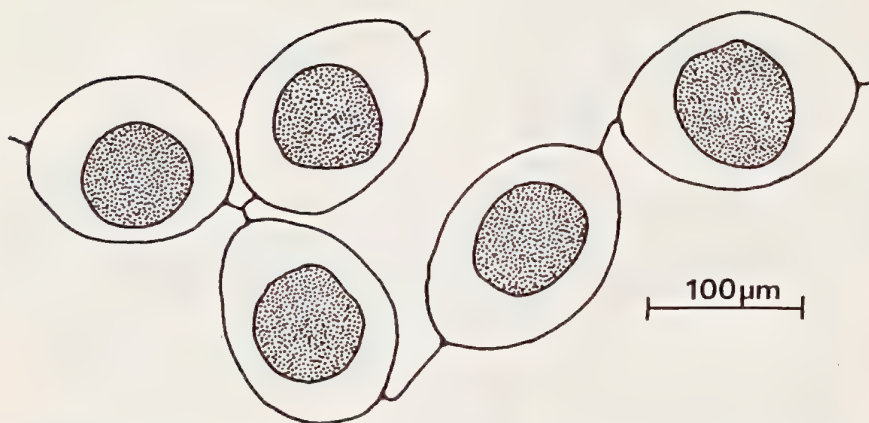


FIGURE 2. *S. diemenensis* : Detail of capsules (containing embryos) which, in the spawn, are embedded in jelly; they are connected into strings by tough threads and sometimes one capsule is connected to two others.

TABLE 2 : Dimensions of encapsulated developmental stages in *S. diemenensis*

Stage	Mean μm	95% Confidence Limit	Standard Deviation	90% Confidence Limits
Uncleaved egg - max. dimension	86	± 1.28	2.7	1.4 \rightarrow 4.9
Two cell " "	112	± 1.05	2.2	1.6 \rightarrow 5.4
Four cell " "	88	± 5.48	6.6	5.9 \rightarrow 130.6
Eight cell " "	94	± 3.03	4.5	3.6 \rightarrow 27.5
Sixteen cell " "	101	± 3.02	6.3	5.0 \rightarrow 19.1
Blastula " "	103	± 1.36	6.1	5.4 \rightarrow 9.6
Gastrula " "	100	± 0.98	4.3	3.8 \rightarrow 6.9
Trochophore " "	95	± 1.03	4.6	4.0 \rightarrow 7.2
Early veliger " "	107	± 0.91	4.1	3.3 \rightarrow 6.0
Mid-veliger - max. shell length	111	± 3.61	13.3	12.9 \rightarrow 27.1
Advanced veliger " "	132	± 2.61	10.1	9.2 \rightarrow 17.6

mantle edge has become detached from the shell allowing velum and foot to be retracted into the shell, at first partially and then completely (Fig.1 I). The lumina of digestive gland, stomach and style sac have opened in preparation for feeding and a few remaining yolky spheres from the digestive gland are often visible in the stomach as they are rotated by the cilia. This marks the end of encapsulated development.

Veligers in the outermost layers of jelly develop most rapidly and constantly rotate inside their capsules by vigorous movements of the velar cilia. Escape from the capsule appears to be facilitated by a softening of the wall which is split open with the velar cilia. Veligers continue to escape until the mass is completely spent, which may be up to a week after the onset of hatching.

Capsule measurements were taken at each developmental stage for a number of egg masses with capsule size expressed as capsule length:width ratio in μm (Table 3). Samples of capsules from

different parts of the same egg mass were measured and found to be of similar size as no significant differences were found using Duncan's Multiple Range Test (Steel and Torrie, 1960). Similarly, results of Duncan's Test performed on ratios of capsules from different masses (at the same developmental stage) indicate that capsule size does not differ significantly at the 0.1% protection level from mass to mass. Capsule ratios compared from egg laying through to hatching using the same test were also shown not to differ significantly.

TABLE 3 : Dimensions of capsules containing mid-veligers in *S.diemenensis* and *S.baconi*

	<i>S.diemenensis</i>		<i>S.baconi</i>	
	Mean μm	Standard Deviation	Mean μm	Standard Deviation
Capsule length	159 (Range 144 - 172)	5.59	206 (Range 180 - 240)	9.41
Capsule width	125 (Range 116 - 136)	4.91	156 (Range 144 - 188)	5.71
Ratio length:width	1.3	0.05	1.3	0.07

Siphonaria baconi

Egg masses raised under the same conditions as those of *S.diemenensis* took longer to develop, from 13 to 16 days. However, masses of this species were found to be more difficult to rear in captivity when collected from the shore after deposition, suggesting that they may be more specific in their ecological requirements. This may be one reason for the much greater success of *S.diemenensis* on most Victorian rocky shores.

TABLE 4 : Mean dimensions of encapsulated developmental stages in *S.baconi*

Stage	Mean μm	95% Confidence Limit	Standard Deviation	90% Confidence Limits
Uncleaved egg - max. dimension	96	± 0.96	2.0	1.3 \rightarrow 4.9
Two cell " "	120	± 1.71	3.6	2.5 \rightarrow 9.6
Four cell " "	125	± 1.85	3.9	3.1 \rightarrow 11.4
Blastula " "	119	± 1.67	7.7	6.8 \rightarrow 13.1
Gastrula " "	111	± 1.0	4.5	3.9 \rightarrow 7.4
Trochophore " "	110	± 0.8	3.1	2.4 \rightarrow 5.9
Mid-veliger - max. shell length	108	± 2.0	4.1	3.3 \rightarrow 12.1
Advanced veliger " "	149	± 3.1	6.7	5.7 \rightarrow 21.7

Development follows the same course as in *S.diemenensis* except for the longer time taken to reach hatching. Dimensions of the various stages are given in Table 4, and again they do not differ significantly from those of *S.diemenensis* (Duncan's Test). Capsule dimensions for *S.baconi* are given in Table 3. Like *S.diemenensis*, capsule ratio does not vary significantly in different parts of the same egg mass, nor from egg laying through to hatching. The mean capsule ratios of *S.baconi* and *S.diemenensis* (at the same developmental stage) do not differ (1:3 for each), although variation in ratios is greater for *S.baconi* (as shown by a standard deviation of 0.07 as against 0.05). Results of Duncan's Test indicate that this difference is not significant.

DISCUSSION

Spawn of *S.diemenensis* and *S.baconi* can be most easily distinguished by size and shape. The spawn ribbon of *S.diemenensis* is of greater height (5.31 mm) and is more uniform in shape (either a horseshoe or a spiral) than that of *S.baconi* which is flatter (1.64 mm) and often irregular in

outline with foreign matter adherent. Voss (1959) has shown that *S.pectinata* from Florida produces spawn in the form of small oval ribbons which are similar in colour and dimensions to those of *S.diemenensis* and *S.baconi* and intermediate between them in height (2 mm). Members of the Family Siphonariidae, therefore, produce jelly masses in ribbons resembling most diotocardian and primitive monotocardian prosobranchs and more primitive opisthobranchs (Anderson, 1960; Fretter and Graham, 1962). Like *S.pectinata* (Voss, 1959), the spawn of *S.diemenensis* and *S.baconi* contains a mass of egg-shaped capsules embedded in a jelly matrix and enclosed by a toughened wall. The capsules of all three species are of similar dimensions when laid and are connected into strands by a fine thread from each end. It is interesting to note that larger egg capsules of almost identical structure are produced by the pyramidellid *Odostomia* (Fretter and Graham, 1962), a prosobranch quite unrelated to *Siphonaria*. Egg-shaped capsules are also produced by members of the opisthobranch genus *Doto* but they are smaller when laid than those of *Siphonaria* and are not connected by threads (Kress, 1975). Kress (1975) also reported occasional twins for *Doto*, but these have not been observed in *Siphonaria*.

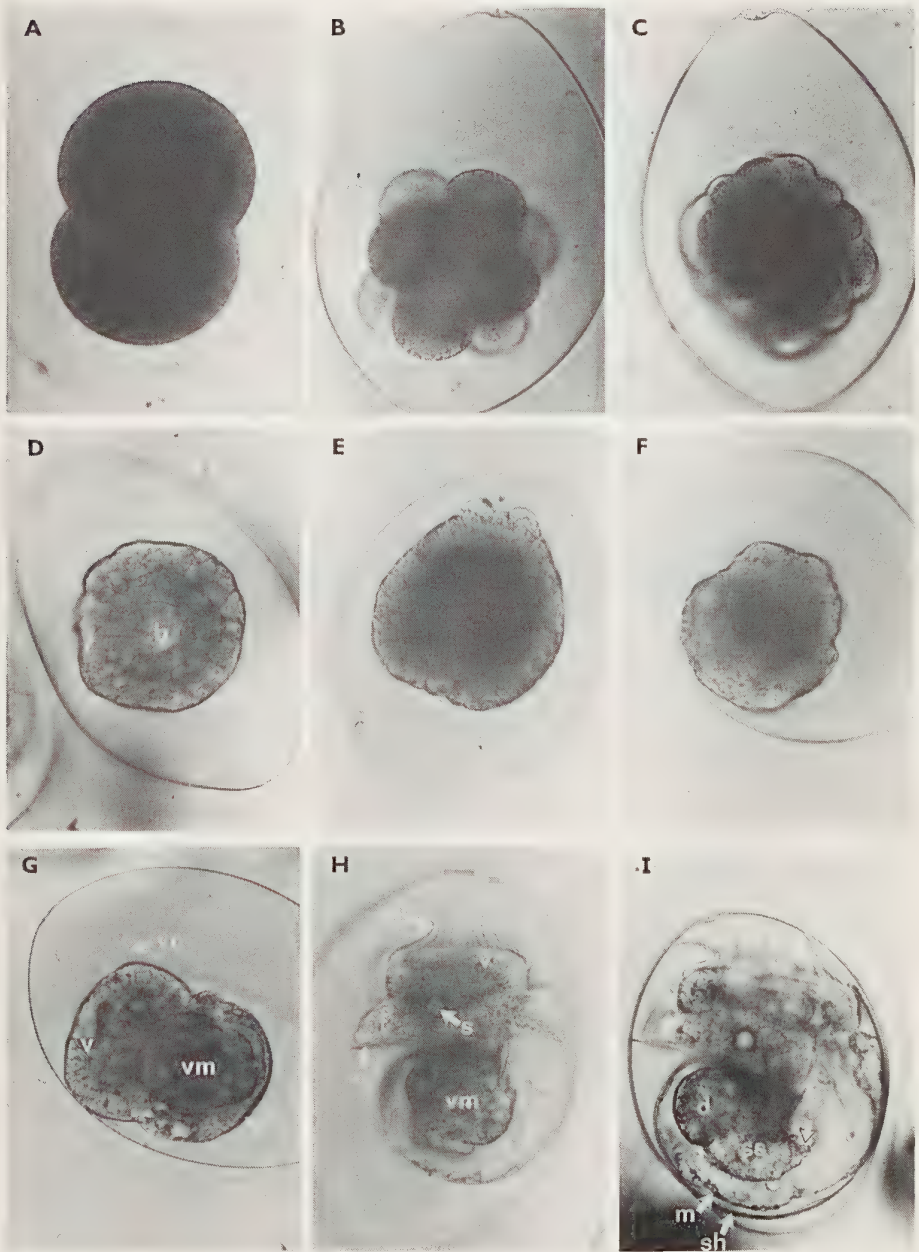
Voss (1959) quotes from Dieuzeide (1935) that development time for *S.pectinata* in Algeria is 20 days at 57 - 75°F but the present results show that development time for the two Victorian species is more rapid (10 to 16 days) at a predominantly lower temperature (15°C, 58°F). The course of development for *S.pectinata* is not described by Voss (1959), but for *S.diemenensis* and *S.baconi* is very similar. Both species lay large numbers of small eggs which hatch into well developed veligers. The gut and other organs of these larvae are highly differentiated, torsion is complete, most of the yolk has already been utilized and the large velar cilia are obviously adapted for a long planktotrophic life. In this respect they resemble the veligers of many monotocardian prosobranchs (Lebour, 1937, 1945; Fretter and Graham, 1962; Fretter and Pilkington, 1970) which may spend up to two months or more in the plankton. Encapsulated embryonic development is similar to that described for the Australian prosobranchs *Bembicium nanum* and *B.auratum* by Anderson (1961, 1962), although *Bembicium* lacks a distinct capsule and Anderson did not record detailed embryonic measurements. Kress (1975) found for the British opisthobranch *Doto* that capsule length to width ratio decreased during development, but this did not occur in *Siphonaria*. However, the length to width ratio of capsules at the same developmental stage was found to be constant for all three *Doto* species, as it is for the two *Siphonaria* species.

Advanced veligers of *S.diemenensis* and *S.baconi* hatch in a similar manner to *S.pectinata* (Voss, 1959). Hatching in the Australian species is also probably stimulated by wetting of the egg mass as Voss found for *S.pectinata*; she suggests that this may be a natural stimulant for ribbons laid above low water.

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FIGURE 3. Series of developmental stages in *S.diemenensis*. Magnification $\times 730$. A, Two cell stage; 2 hours after deposition. B, Eight cell stage; 6 hours after deposition. C, Early blastula; 21 hours after deposition. D, Late blastula showing blastopore (b); 28 hours after deposition. E, Gastrula; 2 days after deposition. F, Trochophore (cilia not visible, but present); 3 days after deposition. G, Early veliger with velum (v) and velar cilia (vc), undifferentiated visceral mass (vm), shell rudiment (sr) (foot not in focus); 4 days after deposition. H, Mid-veliger undergoing torsion showing visceral mass (vm) differentiating, statocyst (s), larger shell (sh) with mantle edge (m) still attached, foot (f) with cilia and projecting operculum (o); 5 days after deposition. I, Advanced veliger, ready to hatch showing stomach with style sac (ss), digestive gland (d), rectum (r), the shell (sh) now filling the capsule and the mantle edge (m) which has detached allowing the veliger to completely retract; 10 days after deposition.



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A REVIEW OF AUSTRALIAN SPECIES OF *AUSTROCYLICHNA*,
NIPPONATYS, *CYLICHNATYS* AND *DINIATYS* (MOLLUSCA:
GASTROPODA: HAMINOEIDAE)

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SUMMARY

Recent and Tertiary species of *Austrocylichna* Burn, *Nipponatys* Kuroda and Habe, *Cylichnatys* Kuroda and Habe, and *Diniatys* Iredale from Australia are reviewed. Seven species are recognized: *Austrocylichna exigua* (A. Adams), *A. leucampyx* sp. nov., *A. lagena* sp. nov., *Nipponatys tumida* sp. nov., *Cylichnatys campanula* sp. nov., *C. darraghi* sp. nov., and *Diniatys dentifera* (A. Adams). The anatomy of the four genera, particularly the form of the gastral plates, indicates their systematic position in the family Haminoeidae. Also, a hitherto misidentified species from Japan is renamed as *Limulatus habei* sp. nov.

INTRODUCTION

The family Haminoeidae is well represented in temperate and tropical Australia, where many species live from the highest intertidal zone to beyond the edge of the continental shelf. Most species occur in the lower intertidal zone and at moderate depths. A few species have very colourful animals, many have drab or dark animals, and many more have slender cream animals adapted to a fully burrowing life.

The first species of Haminoeidae from Australia was described by Gray in 1825 (*Bulla wallisii*, locality 'New Holland', now *Haminoea wallisii* (Gray)). Additional species were described by Quoy and Gaimard (1833), A. Adams (1850, 1854), Angas (1877), Brazier (1877), Watson (1886), Hedley (1904, 1912), Iredale (1936), and Burn (1966). Further species have been recorded or reported upon in the papers of these and other authors. Not all species were well described and figured, nor are all recognizable at the present time.

In a review of the Japanese species of Haminoeidae, Habe (1952) utilized all previous attempts at subdividing the family, and added a number of new generic and subgeneric groupings, not all of which (especially those relating to *Haminoea* s.l.) have met with general acceptance. In a few instances, the radula and gastral plates were described and figured. Zilch (1959) took a more moderate view of Habe's classification, and reduced most of his genera to subgenera, or to synonymy. More recently, Nordsieck (1972) closely followed Zilch's arrangement of the taxonomy, and added yet another subgenus.

Limulatys Iredale, 1936

(= *Tepidatys* Iredale, 1936)

Weinkauffia A. Adams, 1858

Austrocylichna Burn, 1974

Mimatys Habe, 1952

Micratys Habe, 1952

Sphaeratys Nordsieck, 1972

Nipponatys Kuroda and Habe, 1952

Diniatys Iredale, 1936

(? = *Micraenigma* Berry, 1953)

Liloea Filsbry, 1921

Haminoea Turton and Kingston, 1830

Doubtful:

Osorattis Iredale, 1929

Spissitydeus Iredale, 1936

As all these genera (except *Nipponatys*, *Cylichnatys* and *Austrocylichna*) were created solely upon shell characteristics, it is difficult to judge how well they will survive future research. Where the anatomy has been studied, it has generally qualified the divisions based upon the shell. By combination of shell and animal features, the four taxa reviewed here must be regarded as distinct genera.

Genus *Austrocylichna* Burn, 1974:44

Type species: (original designation) *Bulla* (*Atys*) *exigua* A. Adams, 1850.

DIAGNOSIS: Shell of $1\frac{1}{2}$ whorls, ovate, slender, weakly spirally striated anteriorly and posteriorly, smooth medially; vertex concave, shallow or excavate; columella straight, with wide labrum behind which a deep slender umbilicus; posterior aperture projecting well beyond vertex, inner margin twisted.

Animal with head posteriorly bilobed and ridge-like Hancock's organs; foot short, truncate behind, with small parapodia. Jaw elements large; radula with 4.1.1.1.4 teeth, central broad and without cusps, lateral tooth denticulate, marginal teeth slender and smooth; gastral plates three, with transverse straight spiny ribs. Male copulatory organ with high plicae in aetium, and large prostrate gland.

REMARKS: Similarities of the radular teeth to those of the Scaphandridae led to *Austrocylichna* originally being classified in that family. Comparison of its radula, and animal and shell features, with the other genera in this paper induce the writer to transfer *Austrocylichna* to the Haminoeidae. In so doing, special emphasis has been placed upon (1) the twisted inner lip of the posterior aperture, (2) the presence of only $1\frac{1}{2}$ whorls of shell with the inner whorls resorbed or dissolved away, (3) the ridge-like Hancock's organs, (4) the broad base of the central tooth, and (5) the general shape of the chitinous gastral plates and the spiny transverse ribs.

As far as the writer is aware, all species of Scaphandridae retain the innermost whorls and protoconch of their shell at all stages of growth. Lemche (1948) described and figured this part of the shell of many northern Atlantic species, and the writer's experience with Australian scaphandrids confirms Lemche's findings. On the other hand, Marcus (1957, 1958) noted the dissolved or resorbed inner whorls and tightly folded cord of periostracum in *Haminoea elegans* (Gray) from Brazil, and it has since been reported for other species of Haminoeidae (Marcus and Burch, 1965; Burn, 1969; Marcus, 1970, 1972). Resorption of the inner shell occurs in *Austrocylichna* and the other genera reviewed in this paper, and would seem, from the available information, to be a good characteristic of the family Haminoeidae.

The Haminoeidae, and the whole Haminoeacea, have three chitinous gastral plates, each curled under anteriorly and with a rounded projection at each end on the outer side. Transverse ribs, straight or meeting at an angle at the median crest, ornament the inner face of the plates in almost every species. The plates in *Austrocylichna* are of this kind. A few species have superficially smooth plates, but even in these incipient ribs can be seen at the curled under anterior end. In the Scaphandridae, there are three or two calcareous gastral plates, the surface of which is smooth.

In shell shape, *Austrocylichna* belongs to the group of *Atys*, *Aliculastrum*, *Limulatys* and *Weinkauffia*, all with the posterior aperture projecting beyond the vertex and the inner lip twisted. It has not the inflated shape of the first, is umbilicate and more slender than the second, has not the folded columella of the third, nor the abruptly truncated columella of the last. The radula of the type species, *A. exigua*, has a broad smooth-edged central tooth similar to that in *Nipponatys*, but that genus has a smooth lateral tooth whereas in *A. exigua* it is denticulate.

Three species of *Austrocylichna* are distinguished, *A. exigua* (A. Adams) from shallow waters of southern Australia, *A. leucampyx* sp. nov. from eastern Australia, and *A. lagena* sp. nov. from the edge of the southern continental shelf.

Austrocylichna exigua (A. Adams)

Figures 1-7

Bulla (*Atys*) *exigua* A. Adams, 1850:589, pl. 126, fig. 129; Angas, 1878:869
Atys exigua Sowerby, 1869: pl. 4, fig. 19; Pilsbry, 1893:270, pl. 28, fig. 24.
Roxania exigua Tate & May, 1901:417; Pritchard & Gatliff, 1903:213; May, 1921:103; 1923:
 pl. 46, fig. 13; Cotton & Godfrey, 1933:82, pl. 1, fig. 11.
Damoniella exigua Cotton & Godfrey, 1938:33; Macpherson & Chapple, 1951:139; May, 1958:
 pl. 46, fig. 13; Cotton, 1959:406; Macpherson & Gabriel, 1962:246.
Austrocylichna exigua Burn, 1974:46, fig. 1-5; Poore & Rainer, 1974:408.

DIAGNOSIS: Shell of $1\frac{1}{2}$ whorls, small to medium size, thin but solid, elongate ovoid to subcylindrical in shape, rarely angulated at mid-length, slightly narrower posteriorly, diameter less than half length, anteriorly rounded, posteriorly obliquely truncated. Spiral striae strong anteriorly, up to 20 in number, weak posteriorly, up to 8 in number, or obsolete; axial threads not developed. Aperture slender, parallel anteriorly and narrowing to third quarter, posteriorly wider, inner margin twisted and rising sharply from vertex. Columella long, straight or slightly twisted, with wide labrum projecting over slender deep umbilicus. Vertex shallowly concave, sometimes with a crescentic perforation of little depth. Colour of fresh shells translucent with opaque anterior quarter and posterior fifth, of dead shells entirely opaque white; periostracum thin, fragile, yellowish-fawn.

DIMENSIONS:	Length	Diameter	D:L
Holotype (with broken lip)	4.0 mm	2.0 mm	50%
Swan Estuary, W.A.M. (70.2565)	5.7	2.4	42.1
Outer Harbour, S.A.M. (T.D.1042)	5.56 2.74	2.3 1.26	41.4 45.9
Hardwick Bay, A.M. (C13302)	5.5 1.7	2.42 0.8	44.0 47.0
Mallacoota, A.M. (C50562)	4.44	2.2	49.5
Port Phillip, N.M.V. (F30108)	4.42	1.75	39.6
Cape Portland, T.M. (E7746)	2.42 1.5	1.1 0.625	45.4 41.3

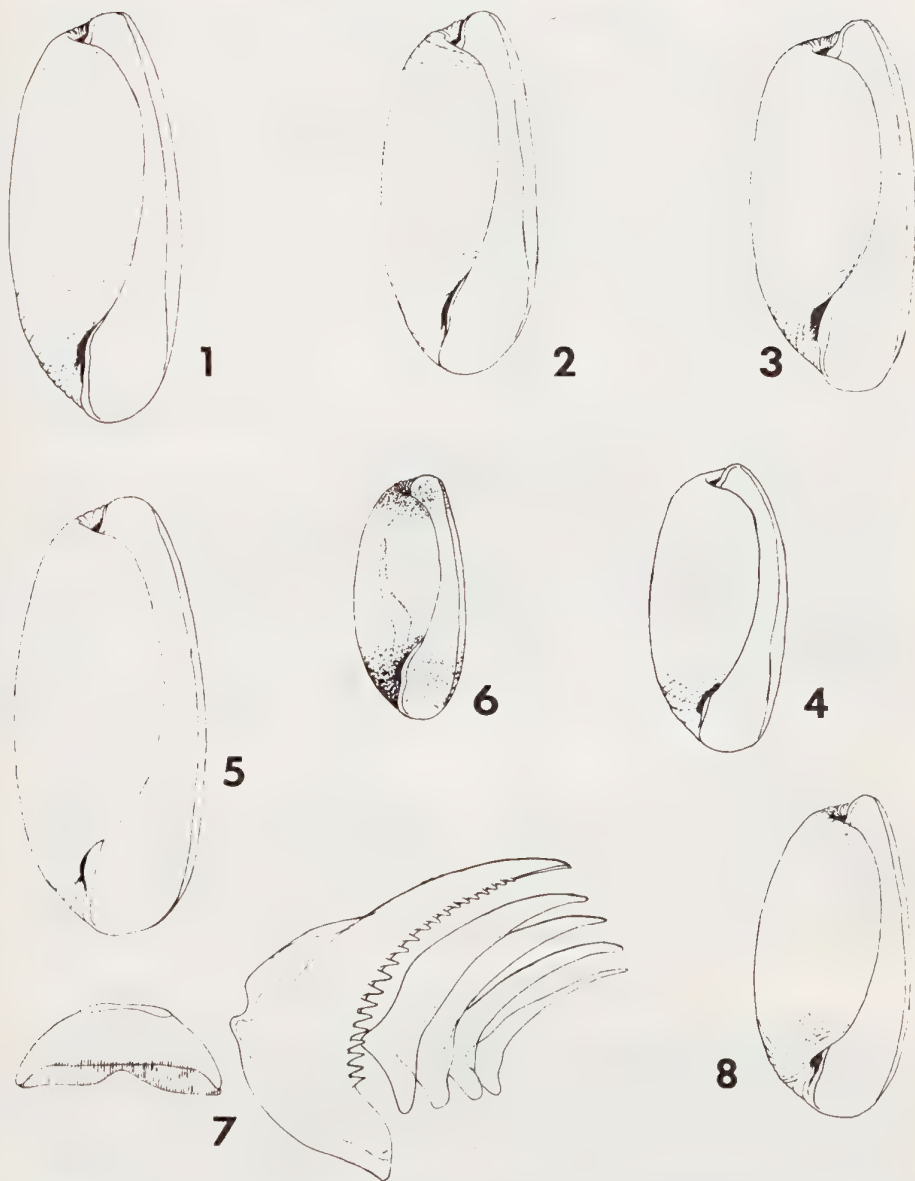
Animal in preservative yellowish-cream with black eyes. Head small, wider than long, with shallow emargination in front edge, bilobed behind, lobes well separated. Hancock's organs a thickened ridge on the body wall below each lobe of head. Seminal furrow with high margins. A broad flat oral lobe each side of mouth, projecting beyond anterior edge of head. Foot short and broad, rounded in front and behind, with small triangular parapodia covering only anterior part of shell; epipodium large, filling posterior aperture. Gill elongate triangular, with 6 transverse bipartite lamellae. Male copulatory organ crosses under oesophagus to left side of head and curls back to median line; atium small and short, with several high plicae distinct from seminal groove which continues through a shorter muscular duct to the soft, bulky prostate gland with wide lumen.

Jaws composed of a pair of areas of few large polygonal elements, similar to that in *Cylichna* *campanula* sp. nov. Radula hyaline, 0.36 mm long, with 23 rows of 4.1 1.1 4 teeth; central tooth with broad striated base and thickened smooth edge, lateral tooth large, 100 μ m long, scaphandroidal in shape with cusp bearing 20-25 large pointed denticles along the edge, marginal teeth slender, curved. Gastral plates 3, haminoeoid in form, each about 0.5 mm long, yellowish, with 10 chevron-like brownish ribs from which pointed elements project. Oesophagus without crop between pharynx and gizzard, nerve ring in front of pharynx.

LOCATION OF TYPE: B.M.N.H. Holotype (19748)

TYPE LOCALITY: Port Lincoln, S.A.

ADDITIONAL MATERIAL EXAMINED: 4 km SSW of Patterson River mouth, Port Phillip, Vic., 8 m in sandy-mud, 1968-1973, coll. Marine Pollution Group, Fisheries & Wildlife Division



FIGURES 1-8.

- 1-7. *Austrocylichna exigua* (A. Adams). 1, Off Lakes Entrance, Vic., 37 m (N.M.V. F30110). 2, Off Portsea, Port Phillip, Vic. (N.M.V. F30109). 3, Off Point Cook, Port Phillip, Vic., 15 m (N.M.V. F27917). 4, Rocky Bay, Swan Estuary, W.A., 3-7 m (W.A.M. 2.74). 5 & 6, Outer Harbour, St. Vincent Gulf, S.A. (S.A.M. T.D.1042). 7, Radular teeth, 4 km SSW of Patterson River mouth, Port Phillip, Vic., 8 m (N.M.V. F27918).
8. *Austrocylichna leucampyx* sp. nov. Woody Point, Moreton Bay, Qld, holotype (N.M.V. F29802).

ALL FIGURES OF SHELLS ARE $\times 12$, EXCEPT FIGURE 11 WHICH IS $\times 25$.

(N.M.V. F27918, 5 preserved spec.). Off Point Cook, Port Phillip, Vic., 15 m, coll. C.J. Gabriel (N.M.V. F27917, 22 spec.). Port Phillip, Vic., coll. T. Worcester, Gabriel Colln (N.M.V. F30108, 2 spec.). Off Portsea, Port Phillip, Vic., coll. C.J. Gabriel (N.M.V. F30109, 1 spec.). Off Lakes Entrance, Vic., 37 m, coll. W.S. Ayres, Gabriel Colln (N.M.V. F30110, 1 spec.). Mallacoota, Vic., coll. R. Bell (A.M. C50562, 1 spec.). White Beach, Tasman Peninsula, Tasm., October 1967, coll. A. Dartnall (T.M. E10102, 1 spec.). D'Entrecasteaux Channel, Tasm. (T.M. 18378/E2843, 1 spec.). Cape Portland, Tasm., 15 May 1970, coll. G. Davis (T.M. E7746, 7 spec.). Aldinga Bay, St. Vincent Gulf, S.A., coll. R. Tate (A.M. 6710, 9 spec.). Hardwick Bay, Spencer Gulf, S.A., coll. W. Bednall (A.M. C13302, 43 spec.). Outer Harbour, St. Vincent Gulf, S.A. (S.A.M. T.D.1042, 10 spec.). Rocky Bay (stn 4), Swan Estuary, W.A., 16 January 1973, coll. P.N. Chalmers & G.W. Kendrick (W.A.M. 274, 1 spec.). Dredge spoil from between old railway and road bridges, Swan Estuary, North Fremantle, February 1964, coll. G.W. Kendrick, (W.A.M. 70 2565, 1 spec. :? Middle Holocene).

DISTRIBUTION AND HABITAT: Eastern Victoria and Tasmania to south Western Australia, ?Middle Holocene to Recent, 8-37 m in fine sandy-mud.

REMARKS: Although considerable variation in shell shape can be seen in the large number of specimens examined, the range of variation is present within single populations and is of no significance. Specimens angulate at mid-length are very uncommon; these are usually large and thickened. Subcylindrical specimens are more common, and could be confused with *Nipponatys tumida* sp. nov. but for the presence of the umbilicus.

A. exigua and *A. leucampyx* sp. nov. are closely allied, but the latter has a shorter columella, wider umbilicus, fewer (10-12) anterior spiral striae, stronger axial sculpture, and lacteous axial bands. The deep-water *A. lagena* sp. nov. is larger and relatively broader, with wide columella and wide umbilicus.

The Holotype, examined in May 1974, is a very dead shell without sculpture, labrum, anterior and outer lips. It compared well with other well worn shells attributed to *A. exigua*, particularly in the shape of the posterior aperture and twisted inner lip, in the long columella, and in the slender deep umbilicus.

In older collections, *A. exigua* has often been confused with *Volvulella rostrata* (A. Adams), hence the literature records cannot be taken as correct. The report by Pritchard and Gatliff (1903: 213) of the species from Westernport is incorrect, their specimens in the N.M.V. from this locality are *Nipponatys tumida* sp. nov.

A single specimen from the top 1 m at the west end of a fresh rock fall at the Pleistocene deposit at Minim Cove, Mossman Park, Perth, W.A. (W.A.M. 77.2222) is very close to small *Nipponatys tumida* sp. nov. in shape and proportions, but differs in the greater infilling of the vertex and the presence of a deep narrow groove behind the short straight columella leading to a slender umbilicus. It differs from *A. exigua* in the broadly ovoid shape and lower posterior lip, yet seems best placed in *Austrocylichna*. More material will be required before any decision can be made regarding the proper placement of this specimen.

Austrocylichna leucampyx sp. nov.

Figure 7

DIAGNOSIS: Shell of 1½ whorls, small to medium size, thin but solid, ovoid to subcylindrical, broadest at anterior third, rarely slightly angular at mid-length, narrowing posteriorly and contracted slightly just below the shoulder, diameter equals half length, anteriorly broadly rounded, posteriorly obliquely truncate. Spiral striae weak, 10-12 shallow striae anteriorly, 2-4 very faint striae posteriorly; axial threads raised, prominent at shoulder and near columella. Aperture slender, anteriorly parallel and narrowing to third-quarter, posteriorly little wider, inner margin slightly twisted and emerging vertically from vertex. Columella short, with shallow truncation at mid-length, with very slender labrum; umbilicus deep and wide. Vertex shallowly concave. Colour translucent white with broad axial milky bands, or entirely dull white.

DIMENSIONS:	Length	Diameter	D/L
Holotype	3.6 mm	1.74 mm	48.3%
Paratypes	3.6	1.82	50.5
	4.6	(broken lip)	---
	3.24	1.78	54.8

Animal not known.

LOCATION OF TYPES: N.M.V. Holotype (F29802) and 7 paratypes (F29803).

TYPE LOCALITY: Woody Point, Moreton Bay, Qld., September 1963, coll. J. Kerslake.

DISTRIBUTION: Known only from type locality.

REMARKS: Judged by the number of specimens in the type series, *A. leucampyx* is not uncommon at the type locality, and ought be found living there. The species is very close to *A. exigua*, but differs by being broadest at the anterior third, by having a shorter columella and wider umbilicus, and by having stronger axial threads.

A. leucampyx is perhaps identical with *Ventomnestia colorata* Iredale (1936) from Sydney Harbour, New South Wales, which species is, according to the description and figure, longer (6 mm) and relatively narrower (2.5 mm or 41.7%), cylindrical in shape with irregularly spaced spiral striae over the whole shell, and cream in colour with a broad pale brown band. Apparently *V. colorata* is known only from its original collection. The systematic position of *Ventomnestia* is doubtful; Iredale (1936) call it a 'Cylichnid' (i.e. Scaphandridae), while Habe (1950 et seq.) has consistently treated it as a genus of the family Retusidae. *A. leucampyx* has only 1½ whorls, therefore is a haminoeid.

The specific taxon, from the Greek leukos – white plus ampyx – headdress, fillet, refers to the axial milky bands of the shell.

Austrocylichna lagena sp. nov.

Figure 9

DIAGNOSIS: Shell with internal whorls, medium to large, fairly solid, subpyriform to subcylindrical, broadest at anterior quarter to third, narrowing posteriorly, diameter more than half length, anteriorly narrowly rounded, posteriorly obliquely truncate. Spiral striae weak, 5-10 shallow striae anteriorly only; axial threads visible but not developed, shell quite smooth. Aperture slender, widest at anterior quarter and narrowing to third quarter, posteriorly very little wider, inner margin slightly twisted and thickened, emerging at a steep angle from the vertex. Columella long, broad with a shallow twist at mid-length, thickened, with very narrow labrum; umbilicus deep and wide. Vertex concave, with or without shallow crescentic perforation. Colour pale fawn or cream.

DIMENSIONS:	Length	Diameter	D/L
Holotype	6.42 mm	3.5 mm	54.5%
Paratype 1	6.875	3.75	54.5
2	5.04	2.83	56.1
Animal not known			

LOCATION OF TYPES: S.A.M. Holotype (D16169) and paratype 1 (D16170). N.M.V. Paratype 2 (F30111).

TYPE LOCALITY: Off Cape Jaffa, S.A., 238 m, 1905, coll. J.C. Verco.

DISTRIBUTION: Known only from type locality.

REMARKS: It is extremely doubtful that *A. lagena* is correctly placed in *Austrocylichna*, or even in the Haminoeidae, because of the retention of all the inner whorls. It is probably a species of Scaphandridae, yet does not easily fit into any existing generic group. Nor can its true systematic position be resolved until the animal is known. It approaches closely the shell from 1200 m off the coast of Portugal, identified by Bouchet (1976: 358) as *Roxania* (?) *semilaevis* (Seguenza), the animal of which is also unknown.

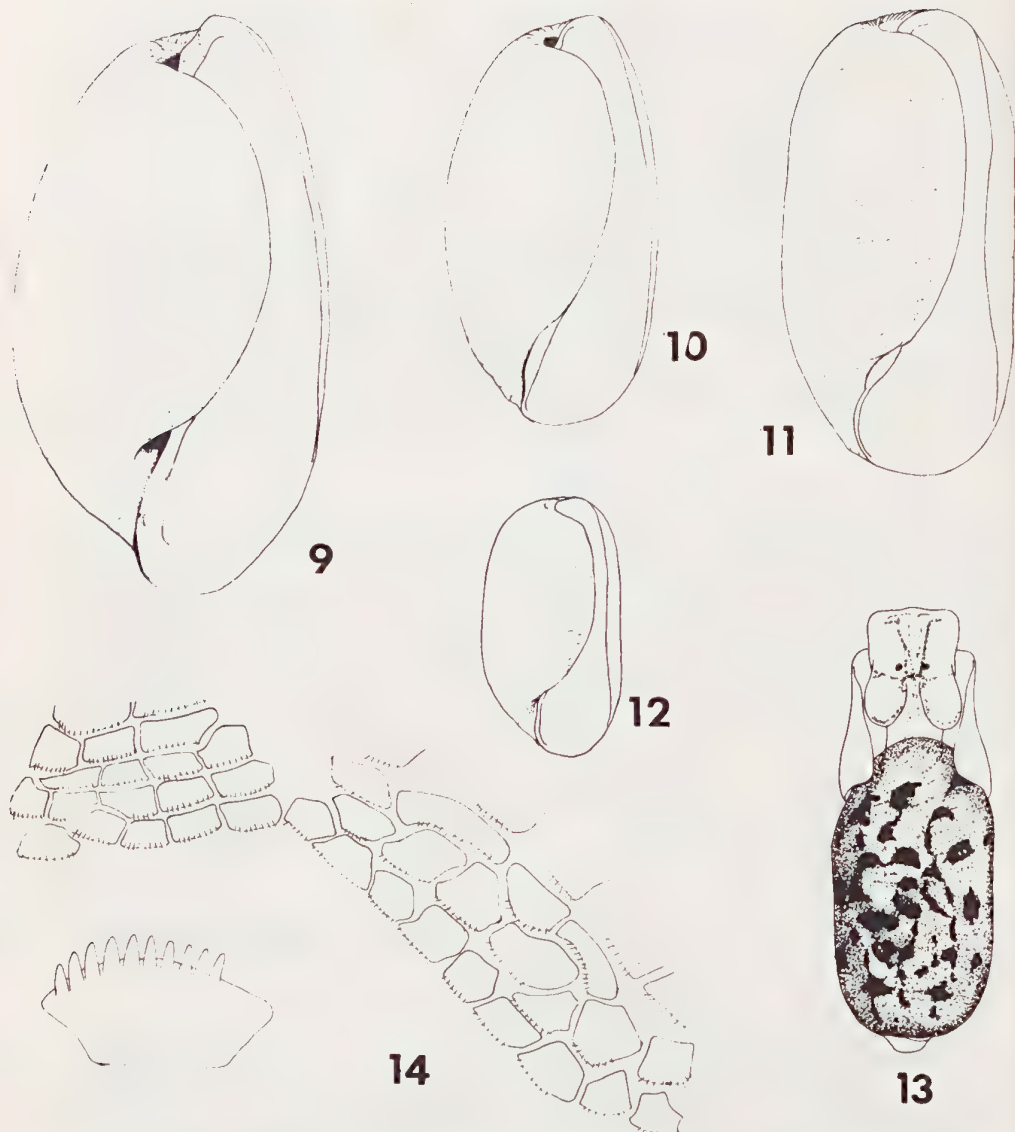
It is of some interest to note that, according to the label with the specimens, Charles Hedley in November 1908 said of this species 'Unknown, on the border between *Atys* and *Cylichna*'.

The specific name, from the Latin *lagena* – a large jar or bottle with handles and a narrow neck, refers to the general shape of the shell.

Genus *Nipponatys* Kuroda & Habe, 1952: 72

Type species: (original designation) *Atys (Alicula) volvulina* A. Adams, 1862.

DIAGNOSIS: Shell of 1½ whorls, ovoid, broadly fusiform, spirally striated anteriorly and posteriorly; vertex perforated or shallowly concave; columella short, oblique, weakly truncate anteriorly; posterior aperture projecting little beyond vertex, inner margin a little twisted.



FIGURES 9-14.

9. *Austrocylichna lagena* sp. nov. Off Cape Jaffa, S.A., 238 m; holotype (S.A.M. D16169).
 10. *Nipponatys tumida* sp. nov. Thompsons Creek at playground, Breamlea, Vic., from spoil excavated from 2 m below water level, holotype (N.M.V. F29798).
 11-14. *Cylichnatys campanula* sp. nov. 11, Rottneest Island, W.A., disused quarry in shell bed, SW corner of Lake Baghdad (W.A.M. 77.81, Middle Holocene). 12, N side of Rocky Point reef, E end of Bluff Road, Yanakie, Corner Inlet, Vic., holotype (N.M.V. F30112). 13, Living animal, Foster Beach, Corner Inlet, Vic. (N.M.V. F30114). 14, Jaw and elements, N side of Rocky Point reef, E end of Bluff Road, Yanakie, Corner Inlet, Vic., paratype (N.M.V. F30113).

Animal unknown Radula with 4-4 teeth per row; central tooth broad and smooth, lateral teeth all of same slender horn-shape and smooth; gastral plates "Atys - type".

REMARKS: The type species, *N. volvulina* (A. Adams), originally collected from 48 m at the island of Tsushima in Korea Strait, is recorded from a number of localities on the Sea of Japan coasts of Kyushu and Honshu, Japan (Habe, 1952). The species was described briefly by A. Adams who likened it to a *Volvulella* with a sunken spire. The shell was first figured by Habe (1952), who also provided information of the radula and gastral plates. The genus and species remain little known.

The short oblique columella, weakly truncate anteriorly, and the smooth central and lateral teeth distinguish *Nipponatys* from other haminoeid genera. In *N. tumida* sp. nov., the weakly truncate columella is seen to be quite abruptly truncate when viewed obliquely across the aperture. The columella is not as strongly built nor so prominently truncated as that of *Diniatys*.

In shell shape, *Nipponatys* is grouped with *Roxaniella*, *Cylichnatys* and *Diniatys*. These genera, and the larger *Liloea*, have a very short, slightly twisted or simply curved inner lip of the posterior aperture, the lip of which projects little beyond the vertex. *Alliculastrum*, to which the type species was originally attributed subgenerically, has a similar oblique columella but is very much larger, the central tooth has a single cusp and incipient lateral cusps, and the lateral tooth is denticulate. The smooth central tooth of *N. volvulina* is like that of *Austrocylichna*, but in that genus the lateral tooth is both differentiated in shape and size, and denticulate, the shell is umbilicate, and the columella straight.

The new species, *N. tumida*, described below, is widely distributed in southern and eastern Australia, apparently still living in the warmer waters of the latter, but extinct in the former area.

Nipponatys tumida sp. nov.

Figure 10

DIAGNOSIS: Shell of variable thickness, broadly ovoid, diameter half length, anteriorly and posteriorly broadly rounded. Spirally striated over whole shell, striations weaker medially, in some specimens striations almost obsolete; axial threads prominent posteriorly at shoulder and anteriorly near columella. Aperture broad anteriorly and narrowing to third-quarter, posteriorly wider, inner margin slightly twisted and rising obliquely from vertex. Columella oblique, straight, weakly and obliquely truncated within aperture, with broad labrum reflected on to body whorl. Vertex shallowly concave. Colour opaque to dull white, periostracum thin, pale brown, darker brown in striations.

DIMENSIONS	Length	Diameter	D:L
Holotype	4.6 mm	2.36 mm	51.3%
Largest paratype	5.04	2.375	47.1
Largest specimen (Barwon Heads)	6.0	2.83	47.3
Smallest specimen (Roches Beach)	1.72	0.92	53.5

Animal not known

LOCATION OF TYPES: N.M.V. Holotype (F29798) and 5 paratypes (F29799). 1 paratype in A.M. (C65697), S.A.M. (D16171), and W.A.M.

TYPE LOCALITY: Thompsons Creek at playground, Breamlea, Victoria, from spoil excavated from 2 m below water level, 1975-1977, coll. R. Burn and K.N. Bell. Middle Holocene.

ADDITIONAL MATERIAL EXAMINED: Woody Point, Moreton Bay, Qld, September 1963, coll. J. Kerslake (N.M.V. F29795, 1 spec.). Barwon Heads, Vic., from gas main excavation on N. side of road 2 km along Geelong road, 1975, coll. R. Burn and K.N. Bell (N.M.V. F29797, 20 spec.), Middle Holocene. Off "The Nits", Phillip Island, Westernport, Vic., 2 m in soft mud and *Zostera*, coll. R. Burn and R. Plant (N.M.V. F29796, 3 spec.). Off Rhyll, Phillip Island, Westernport, Vic., Gabriel Colln (N.M.V. F29801, 2 spec.), Gatliff Colln (N.M.V. F29800, 2 spec.). Great Taylor Bay, South Bruny Island, Tasm., in mud, coll. A. Dartnall (T.M. E5364, 1 spec.). Roches Beach, Frederick Henry Bay, Tasm., 26 February 1964, coll. E. Turner (T.M. E3287). Frederick Henry Bay, Tasm., (Q.V.M. 1977/9/1).

DISTRIBUTION AND HABITAT: Southern Queensland to south-eastern Tasmania, Middle Holocene to Recent, shallow water with soft mud bottom.

REMARKS: There is little variation in the shell throughout the range of this species. Some bigger specimens are slightly less ovoid than the Holotype, and smaller specimens are slightly more ovoid. Some specimens have a more pronounced profile of the posterior lip. Rarely, specimens of *Austrocylichna exigua* from South and south Western Australia are as broad as *N. tumida*, but the latter is immediately distinguished by the oblique columella, the wide labrum, and the absence of an umbilicus. The spiral striations vary a great deal in prominence, from almost obsolete in the type series, to about 10 quite strong anterior striae, to both anterior and posterior striae (Woody Point specimen), to wholly striate (Barwon Heads). From the latter locality, one specimen is quite strongly wholly striate, the striae being equally spaced and alternately broad and deep, narrow and shallow.

N. tumida is closely related to the Japonic *N. volvulina* (A. Adams), but differs in being larger and not as broad, with a lower profile of the posterior lip and a shallower vertex. The sculpture in *N. volvulina* is more pronounced in the figure given by Habe (1952).

Until the discovery of the Moreton Bay specimen with intact periostracum, it was presumed that this species was extinct in Australian waters. None of the specimens from marine localities in Victoria and Tasmania have the appearance of coming from present-day living populations. Where details of collection are available, these indicate recovery from deep within mud, some perhaps dredged from submarine Middle Holocene beds. The type locality, and that at Barwon Heads, both rich in opisthobranch species still living along southern Australian shores, are inland from present coastlines, and are thought to be Middle Holocene in age.

Genus *Cylichnatys* Kuroda & Habe, 1952:51

Type species: (original designation) *Bullinella striata* Yamakawa, 1911 (= *Haminea angusta* Gould, 1859).

DIAGNOSIS: Shell of 1½ whorls, cylindrical or ovoid, weakly striated over entire shell; vertex shallowly concave but not perforated; columella short, curved; posterior lip projecting very little beyond vertex, inner lip simply curved.

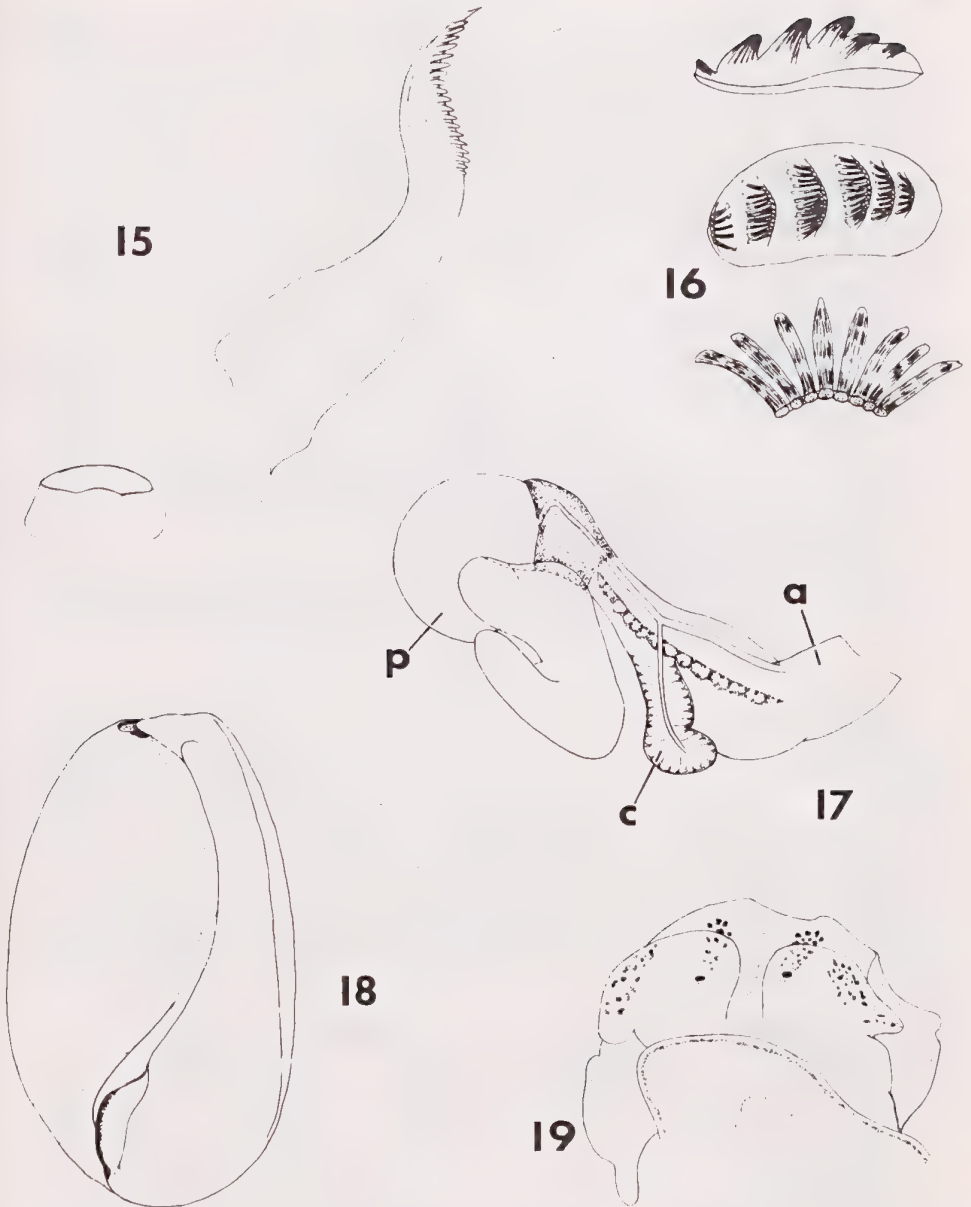
Animal (of *C. campanula* sp. nov.) with subquadrate head, bilobed posteriorly, and with ridge-like Hancock's organs; foot short, truncate behind with small parapodia; epipodium filling posterior aperture, not projecting beyond shell; oral lobes with low sensory papillae. Jaws slender, elements polygonal, denticulate; radula with 1.1.1 teeth, central tooth small, cuspidate or smooth, lateral tooth long, slender, with many fine denticles on inner side and tip; gastral plates three, with chevron-like transverse spiny or knobby ribs. Male copulatory organ comprises long atrium with short caecum at mid-length and long tubular prostate gland.

REMARKS: The narrow radula, slender lateral teeth with comb-like denticles on the inner side, and the entirely striate shell characterize *Cylichnatys*. Some species of *Liloea* have the shell entirely striate, but that genus grows to a much larger size, the radula is always broad, and the male copulatory organ is complex with penial papilla, prostate gland and seminal vesicle, and a pair of larger accessory appendages. Sensory papillae on the oral lobes have not been reported elsewhere among the Haminoeidae, but appear to be analogous to the sensory papillae of the Aglajidae.

Cylichnatys is close to, if not identical with *Roxaniella* Monterosato, 1884 from the Mediterranean. Jeffreys' figures (1856: pl. 2, fig. 18-19) of his species, the type of the genus and now called *R. jeffreysi* Weinkauff (1866), are similar to both *C. angusta* and *C. campanula*. The animal of *R. jeffreysi* is not known.

The species described and figured as *R. jeffreysi* by Nordsieck (1972: p. 30, pl. O IV, fig. 24) is slender with an elongate aperture and definite twist of the columella, and quite unlike Jeffreys' figures. Nordsieck's shell is very likely a new species of *Atys*, closely related to *A. macandrewi* E.A. Smith (1872). Specimens in the N.M.V. collection, from Madiera, labelled *Atys jeffreysi* Weinkauff are not that species, but are really *Atys macandrewi* Smith (1872). Marcus (1970) gave some anatomical details for the latter, together with references and distributional data.

Cylichna grimaldii Dautzenberg (1891) from Dakar, Senegal has recently been referred to *Cylichnatys* (Bouchet, 1977:71). Examination of preserved specimens from the same locality, kindly presented by Dr. P. Bouchet, indicates that this species belongs to neither *Cylichna* nor *Cylichnatys*. Its shell is large and entirely striate, the radula is broad, and the male copulatory organ is complex, all features suggesting a close relationship to *Liloea*.



FIGURES 15-19.

- 15-17. *Cylichnatys campanula* sp. nov., N side of Rocky Point, E end of Bluff Road, Yanakie, Corner Inlet, Vic., paratypes (N.M.V. F30113). 15, Central and lateral radular teeth. 16, Inner face and lateral aspect of gastral plate, and detail of a single rib. 17, Male copulatory organ (a - atrium, c - caecum, p - prostate).
18. *Cylichnatys darraghi* sp. nov., excavation for sewerage tunnel, 12.2 m from surface, below Wright Street, N of Centre Road, Bentleigh, Vic., Black Rock Sands, Cheltenhamian (Upper Miocene/Lower Pliocene), holotype (N.M.V. P48912).
19. *Diniatys dentifera* (A. Adams), head of preserved specimen, Dongara, W.A. (N.M.V. F30118).

Kuroda, Habe & Oyama (1971) give an extensive bibliography and synonymy for *Cylichnatys angusta* (Gould, 1859), which is well-known in Japan from 5-50 m on muddy bottoms in bays, and as a Pleistocene fossil. It is reported as a common species in 10-20 m in the inner bay area of Isumo Bay, Noto Peninsula, Japan (Habe, 1973). The type specimen of *Haminea angusta* in the United States National Museum (Johnson, 1964) is a badly damaged ovoid shell, barely agreeing with the description by Gould (1859) as "ovate-cylindrical, widened in front, obtusely rounded". Figured specimens, notably those in Habe (1961 and 1964 : pl. 42, fig. 23) and in Kuroda, Habe and Oyama (1971: pl. 115, fig. 1) agree with the original description, whereas another figure (Habe, 1952: pl. 20, fig. 14) shows a decidedly cylindrical shell shape. Specimens in the N.M.V. collection (F29794), from the A. Adams Collection purchased from R.F. Geale in 1870, are from the type locality, Simoda, Japan: Geale labelled them *angustata* from Simonda, following Sowerby (1869) whose errors with this species were carefully corrected by E.A. Smith (1872:348).

As well as pointing out Sowerby's transcription error of writing *angustata* for *angusta*, E.A. Smith (1872:346) described *Atrys angustata* from the Gulf of Suez. This has since been regarded as a juvenile of, and relegated to the synonymy of *Aliculastrum cylindricum* (Helbling) (Pilsbry, 1894 : 265). Habe (1952 : 140, pl. 21, fig. 21) and subsequently (1954 : 304, pl. 38, fig. 22; 1955 : 62) included *Limulatys angustata* (Gould, 1859) in his lists of Japanese species. Because this specific name is an incorrect subsequent spelling by Sowerby of the taxon *angusta* (Gould, 1859), it has no status in nomenclature (I.C.Z.N., Article 33(b)). As *Limulatys angustata* (Gould, 1859) is obviously distinct from *Cylichnatys angusta* (Gould, 1859), it is here named *Limulatys habei* sp. nov. The specimen figured from Sōyō-maru Station 4, off Katsuura, Bōsō Peninsula, Japan, 287 m, 16 June 1926, is designated as the holotype.

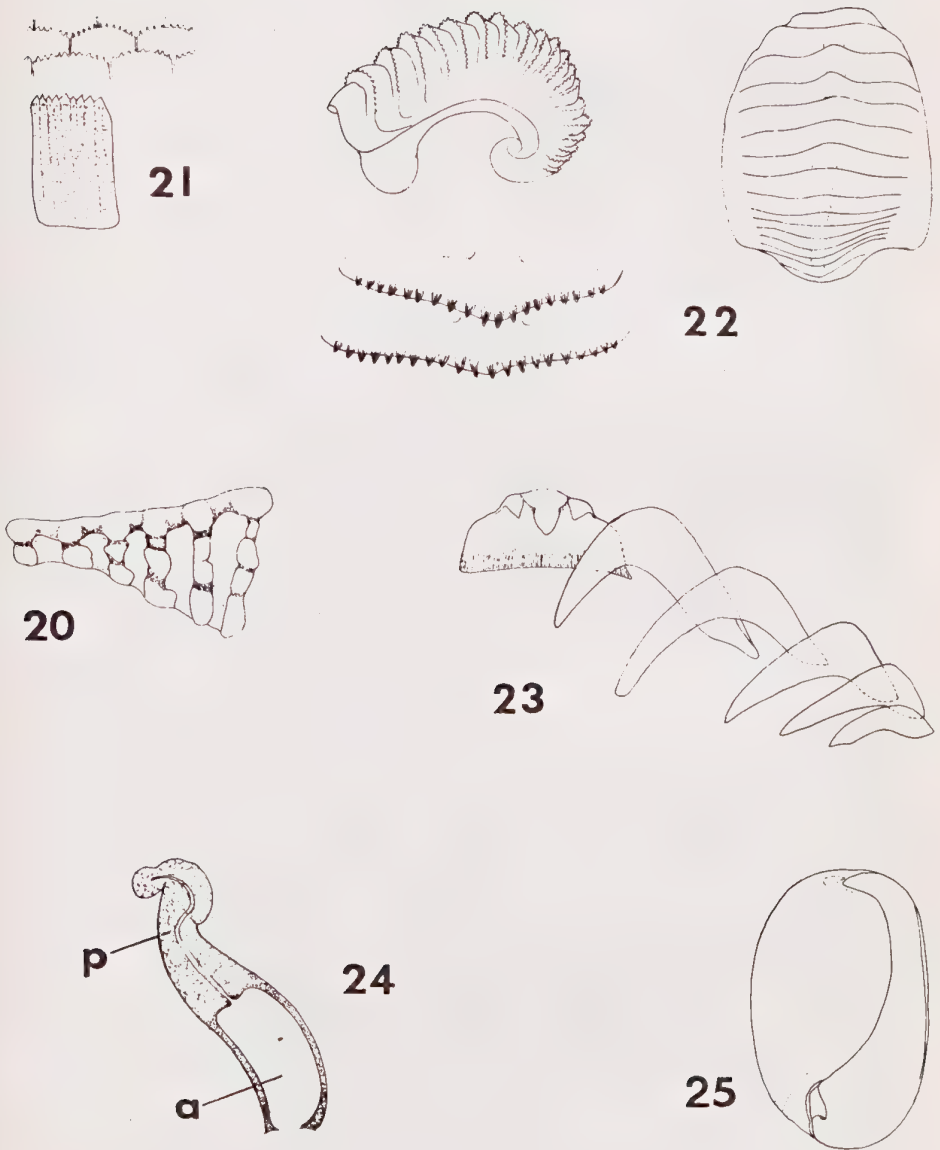
Two Australian species are described, *C. campanula* sp. nov. from living populations along the southern Australian coastline and from Pleistocene and Middle Holocene deposits, and *C. darraighi* sp. nov. from strata of the Miocene-Pliocene boundary in the Tertiary of Victoria.

Cylichnatys campanula sp. nov.

Figures 11-17

DIAGNOSIS: Shell of 1½ whorls, thin to fairly solid, cylindrical to broadly ovoid, broadest at mid-length, diameter generally half, but varying from one-third to two thirds of length, broadly rounded at both ends, sometimes more or less truncate posteriorly. Spiral striae strong to weak, generally narrow, wavy and shallow, occasionally broad, straight and rather deep, with or without raised axial threads crossing the striae, which if present create a secondary reticulation, striae about 40 in number, stronger anteriorly, posteriorly obsolete in some specimens; axial threads sometimes prominent anteriorly and at vertex. Aperture broad anteriorly, narrower and parallel posteriorly, inner margin simply curved, rising very obliquely from vertex. Columella short, curved, very little thickened, labrum small, at junction of columella and body whorl. Vertex very shallowly concave. Colour transparent with opaque anterior and posterior ends in living and fresh shells, opaque white in dead shells; periostracum very thin, yellowish.

DIMENSIONS:	Length	Diameter	D/L
Holotype	2.9 mm	1.57 mm	54.1%
Paratypes	3.14	1.62	51.5
	2.96	1.42	47.3
Cape Portland, Tasm.	3.76	1.36	36.2
(T.M. E7747)	1.04	0.6	57.7
Hardwick Bay, S.A.			
(A.M. C13311)	2.6	1.28	49.2
Cockburn Sound, W.A.			
(W.A.M. 597.77)	2.24	1.14	50.9
Rocky Bay, W.A.			
(W.A.M. 241.73)	3.32	1.52	45.8
Rottneest Island, W.A.			
(W.A.M. 77.208)	2.58	1.46	56.6



FIGURES 20-25

20-25. *Diniatys dentifera* (A. Adams), Dongara, W.A. 20, Hancock's organ from left side of head (N.M.V. F30118), 21, Jaw elements and single element (N.M.V. F30118), 22, Aspects of gastral plates and detail of a single rib (N.M.V. F30118), 23, Central and lateral radular teeth (N.M.V. F30118), 24, Male copulatory organ (a - atrium, p - prostate) (N.M.V. F30118), 25, Shell (W.A.M. 1879-69).

Animal translucent greyish with opaque pigment cells, prominent black eyes, brownish-red speckling on Hancock's organs, and reddish gut in mid-line of head; spots and patches, sometimes large areas, of black pigment on inner surface of dorsal wall of pallial cavity, visible dorsally through shell. Head subquadrate, with sinuate anterior edge and paired posterior lobes, Hancock's organs ridge-like, low. Each side of mouth a rounded oral lobe, bearing an elongate triangular area of crimson-coloured scattered low papillae, probably sensory in use. Foot short and broad, truncate in front and behind, with small parapodia touching only anterior part of shell; epipodium filling posterior aperture and not extending beyond shell, used in crawling. Pallial cavity apparently devoid of branchia. Male copulatory organ crosses under pharynx to left side, with prostate gland filling most of space between pharynx and gizzard, a little more than 1 mm straightened out; atrium slender, thin, with long muscular thickenings; short, bent caecum with deeply folded epithelium branches off at mid-length of atrium; lumen of atrium continues through soft fleshy section at Fundus to folded tubular white prostate gland.

Jaws formed of two narrow strips, each 180 μm long and 40 μm wide or about 12 elements long by 3-4 rows of elements deep; elements large, polygonal, with up to 12 denticles along longest margin. Radula with 16-17 rows of 1.1:1 teeth, central tooth narrow with smooth edge 20 μm wide, lateral tooth 100 μm long, slender and somewhat twisted with 18-20 comb-like denticles along edge to cusp. Gastral plates three, haminoeid in shape but rather flattened on the outer face, about 340 μm long, with 5-7 high chevron-like transverse knobby ribs, each built up by 3-12 curved rods visible within each plate, in colour dark brown or pale with dark ribs.

LOCATION OF TYPES: N.M.V. Holotype (F30112, preserved spec.) and 4 paratypes (F30113, 3 preserved spec. and 1 shell). One paratype (Shell) in W.A.M., S.A.M., and A.M. (C65698).

TYPE LOCALITY: *Zostera* and mud flats, N side of Rocky Point reef, E end of Bluff Road, Yanakie, Corner Inlet, Vic., 11 April 1971 and 1 April 1972, coll. K.N. Bell.

ADDITIONAL MATERIAL EXAMINED: Foster Beach, Corner Inlet, Vic., *Zostera* and mud flats, 22 March 1974, coll. R. Burn (N.M.V. F30114, 1 preserved specimen). Port Albert, Corner Inlet, Vic., *Zostera* and mud flats at swimming area, 15 April 1978, coll. R. Burn & K.N. Bell (N.M.V. F29804, 3 preserved specimens and 1 shell). Wallagarough River, at bridge on Fairhaven Road, near Mallacoota, Vic., 20 February 1973, coll. B.J. Smith and R. Plant (N.M.V. F30115, 8 preserved specimens). Pambula, N.S.W., coll. Mrs. Forde (A.M. C11775, 1 juvenile spec.). Tasmania, 1886, coll. C.E. Beddome, Helms Colln (A.M. C87690, 1 spec.). Cape Portland, Tasm., 15 May 1970, coll. G. Davis (T.M. E7747, 25 spec.). Spring Beach, near Orford, Tasm., 2 February 1970, coll. E. Turner (T.M. E7568, 1 spec.). N of Mt. Younghusband, St. Peters Island, Nuyts Archipelago, S.A., *Zostera* and mud at low tide, January 1978, coll. D. Howlett (N.M.V. F30116, 1 spec.). Hardwick Bay, Spencer Gulf, S.A., coll. H.L. Kesteven (A.M. C13311, 15 spec.). Rocky Bay (stn 3), Swan Estuary, W.A., 7-9 m in western channel, 16 January 1973, coll. P.N. Chalmers & G.W. Kendrick (W.A.M. 3.74, 6 spec.). Rocky Bay (stn 4), Swan Estuary, W.A., 3-7 m on slope at W end of sand bank, 16 January 1973, coll. P.N. Chalmers & G.W. Kendrick (W.A.M. 241.73, 25 spec.). Approx 3 km N of Rockingham, Cockburn Sound, W.A., 18 m mud bottom, 16 January 1965, coll. R. Slack-Smith & G.W. Kendrick (W.A.M. 597.77, 74 spec.).

FOSSIL RECORDS: MIDDLE HOLOCENE: Rottnest Island, W.A.; disused quarry in shell bed, SW corner of Lake Baghdad, 6 January 1977, coll. G.W. Kendrick (W.A.M. 77.81, 81 spec.); quarry at E end of Lake Baghdad, site 2, 5 January 1977, coll. G.W. Kendrick (W.A.M. 77.387, 51 spec.); quarry at E side of Government House Lake, 6 January 1977, coll. G.W. Kendrick (W.A.M. 77.428, 9 spec.); spit at junction between Serpentine and Government House Lakes, 10 January 1977, coll. P.E. Playford (W.A.M. 77.493, 34 spec.); island at E end of Herschel Lake, 6 January 1977, coll. G.W. Kendrick (W.A.M. 77.208, 69 spec.); quarry at E end of Lake Baghdad, 5 January 1977, coll. G.W. Kendrick (W.A.M. 77.299, 39 spec.). Point Waylen, Attadale, W.A.; excavation depth 80-100 cm, 2 March 1971, coll. G.W. Kendrick (W.A.M. 76.2450, 3 spec.); excavation depth 100-120 cm, 2 March 1971, coll. G.W. Kendrick (W.A.M. 76.2316, 7 spec.). Swan Estuary, opposite Roberts Road, Attadale, W.A., dredge spoil, 31 March 1966, coll. G.W. Kendrick (W.A.M. 70.2342, 1 spec.). Swan Estuary, Como, W.A., dredge spoil from between Preston and Thelma Streets, 2-3 March 1972, coll. G.W. Kendrick (W.A.M. 72.166, 1 spec.). Beckenham, W.A., 3 Wimblond Street, excavation between house and Canning River, 1.5-3 m deep, 1966, coll. J. Horwood (W.A.M. 70.2384, 1 spec.). East Rockingham, W.A., well on E side of Mandurah Road, 28 July 1959, coll. G.W. Kendrick (W.A.M. 76.557, 7 spec.). Barragup Bridge, E of Mandurah on road to Pinjarra, W.A., Main Roads

Department bore stn 776.60, depth 3.75-4 m, 3 March 1976, coll. M. Willey & M. Limb (W.A.M. 76-2698, 21 spec.). Lake Clifton, W.A.; lake bed on E side adjacent to old cement factory site, one spade depth, 14 January 1962, coll. E.P. Hodgkin & G.W. Kendrick (W.A.M. 75-254, 44 spec.); *Agonis* thicket on E side, near old cement factory, from an excavation in apparently undisturbed ground, about 0.5 m below surface, 14 January 1962, coll. E.P. Hodgkin & G.W. Kendrick (W.A.M. 76.606, 12 spec.). Australind, near Collie River bridge on Bunbury Road, W.A., dredge spoil from channel deepening deposited along bank, 30 March 1969, coll. H. Merrifield (W.A.M. 75.342, 1 spec.). Leschenault Inlet, W.A., west side, from inlet borehole no. 3 at 10.0 - 11.5 m below present sea level, 1974, coll. R. Barnes (W.A.M. 74.217, 4 spec.). PLEISTOCENE: Minum Cove, Mosman Park, W.A.; W end at fresh rock fall, top 1 m, 27 February 1966, coll. G.W. Kendrick (W.A.M. 77.1344, 18 spec.); lower sample, October 1955, coll. G.W. Kendrick (W.A.M. 69.1507, 5 spec.). Peppermint Grove, W.A., near Scotch College boatshed, 1965, coll. G. Byrne (W.A.M. 68.878, 8 spec.); 12 April 1968, coll. G.W. Kendrick (W.A.M. 68.950, 1 spec.); 14 June 1972, coll. G.W. Kendrick (W.A.M. 77.2518, 2 spec.; N.M.V. P48911, 10 spec.).

DISTRIBUTION AND HABITAT: Southern N.S.W. Victoria E of Wilsons Promontory and eastern Tasmania, and St. Vincent Gulf, South Australia to the Swan Estuary, south Western Australia, Pleistocene to Recent, intertidal *Zostera* and mud flats to 18 m on mud.

REMARKS: *C. campanula* is very close to the small specimens of *C. angusta* (Gould) from Simoda, Japan, in the collection of the National Museum of Victoria (N.M.V. F29794), from which the shell is distinguished only by the courser sculpture and the presence of the small labrum. *C. angusta* grows much larger, a specimen from Obama Bay, Honshu figured by Habe (1952: pl. 20, fig. 14) measured 7.3 x 3.7 mm, another from Sagami Bay figured by Kuroda, Habe and Oyama (1971: pl. 115, fig. 1) measured 8.3 x 4.4 mm. *C. campanula* further differs from *C. angusta* in the absence of a cusp on the central radular tooth, the larger base of the lateral tooth, and the oval shape of the gastral plates. *C. angusta*, like *C. campanula*, has only 1½ whorls of shell.

There is a consistent degree of variation in the shell of *C. campanula* over its distribution along the southern coast of Australia and in its fossil record. Shell shape varies from cylindrical to ovoid and sculpture from weak to strong. Though specimens from eastern Victoria and Tasmania tend to be more cylindrical and less strongly sculptured, similar shells occur within populations from South and Western Australia, and therefore cannot be distinguished. The animal, known only from eastern Victoria and western South Australia, shows no differences.

In some older collections from Tasmania and South Australia, *C. campanula* was found confused with juvenile specimens of *Retusa* spp., but is separated by the open shape of the posterior aperture, the shallow vertex, and the presence of 1½ shell whorls.

Prior to the discovery of *C. campanula* alive in 1971, the species was not known from Victoria, nor is it present in the Gatliff, Gabriel or general collections in the National Museum of Victoria. At the present time, the species apparently does not occur along the Victorian coastline W of Wilsons Promontory, for despite much assiduous collecting in Westernport and Port Phillip, no specimens have been found, either dead or alive. Nor has the species been found during extensive studies of Middle Holocene beds in central and western Victorian coastal areas. It is therefore possible, though unlikely, that *C. campanula* is a species that has only very recently colonized the eastern Victorian coastline. Against this, however, must be judged the earliest collecting record of the species, that by C.E. Beddome from Tasmania in or prior to 1886, indicating that it has been in south-eastern Australia for a relatively short time at least.

C. campanula has a fairly long record from Pleistocene to Recent in Western Australia, although as yet no living specimens have been reported, nor has it been found along the southern coast E of Cape Leeuwin. In South Australia, the species has been found alive at St. Peters Island in the west, and dead in both Spencer and St. Vincents Gulfs, but appears to be absent from the SE of the State. In all probability, *C. campanula* is a species which in the Pleistocene or earlier was distributed along the whole southern coastline, but which, due to changes in coastline and temperature, now persists in an eastern and a western population, separated by a gap of 1000 km of relatively colder water.

The occurrence of *C. campanula* in the Wallagaraugh River, at the bridge on the Fairhaven Road, near Mallacoota, suggests that the species can tolerate a large range of salinities. The Wallagaraugh River at this point is 18 km from the sea, and within sight of the rock sill that marks the termination of estuarine conditions in the river. At the time of collection, the height of a

dry Australian summer, the estuary system of which this river is part had a salinity almost equal to that of the open sea, and a number of marine molluscs were able to rapidly populate the whole of the estuary, apparently to its uppermost reaches.

Salinity tolerance and the ability to rapidly populate help explain the present Middle Holocene and Pleistocene occurrences of the species in the Perth area of Western Australia.

The species is named for Mr K.N. Bell of Stony Creek, Victoria, who first discovered it alive (Latin *campanula* - a little bell).

Cylichnatys darraghi sp. nov.

Figure 18

DIAGNOSIS: Shell with internal whorls, medium to large, solid, ovoid, broadest at mid-length, slightly narrower posteriorly, diameter more than half length, anteriorly broadly rounded, posteriorly narrowly truncate. Spiral striae weak, up to 30 striae anteriorly, closer and deeper near columella, and up to 8 striae posteriorly; axial threads not developed, shell smooth. Aperture broad anteriorly, narrowing posteriorly then parallel; inner margin of posterior aperture thickened, simply curved, rising laterally from vertex. Columella short, curved, thickened; labrum large, very strong and thickened, in many larger specimens projecting ventrally from columella as a sharply raised ridge. Vertex completely filled in and level with body whorl, in some large specimens an eroded curved furrow is present dorsally around the edge of the vertex. Colour, that of the matrix, light orange brown.

DIMENSIONS:	Length	Diameter	D/L
Holotype	5.42 mm	3.17 mm	58.4%
Paratypes	6.41	3.5	54.6
	5.5	3.0	54.5
	3.21	1.875	58.4
	3.175	1.83	57.6

DIMENSIONS: N.M.V. Holotype (P48912) and 118 paratypes (P48913)

TYPE LOCALITY: Excavation for sewerage tunnel, 12.2 m from surface, below Wright Street, N of Centre Road, Bentleigh, Vic., coll. T.A. Darragh and H.E. Wilkinson; Black Rock Sands, Cheltenhamian, Upper Miocene/Lower Pliocene.

DISTRIBUTION: Known only from type locality.

REMARKS: As with the systematic position of *Austrocylichna lagena* sp. nov., the presence of complete internal whorling mitigates against the placement of *C. darraghi* sp. nov. in *Cylichnatys*, which genus it otherwise closely resembles. Comparison with all Tertiary and Recent Australian cephalaspidean opisthobranchs reveals no close relationships, nor is it close to any of the world's species in the available literature. It is most probably a species of Scaphandridae, possibly of the group of genera that includes *Cylichnella*, *Cylichnium* and *Taita*.

The species is named for Mr T.A. Darragh, Acting Director, National Museum of Victoria, and President of the Malacological Society of Australia, who collected the only known series of specimens.

Genus *Diniatys* Iredale 1936:329

Dinia H. & A. Adams, September 1854:21 (non Walker, May 1854).

Type species: (original designation) *Bulla (Atys) dentifera* A. Adams, 1850.

DIAGNOSIS: Shell of 1½ whorls, ovoid, broad; finely spirally striate, vertex shallow, not perforate; columella abruptly truncate, ending with a tooth-like projection, umbilicus not present; posterior aperture projecting little beyond vertex, inner lip simply curved.

Animal with subquadrate head bilobed posteriorly with lobes folded forward on to head, and with vertically plicate, large triangular Hancock's organs; foot short, truncate behind, with small parapodia; epipodium filling posterior aperture but not projecting as tail. Jaw elements oblong, with rounded denticulate edge; radula with 5.1.5 teeth, central tooth broad with three cusps and striated base, lateral teeth all of same slender hammer-shape and smooth; gastral plates three, with slightly arched transverse spiny ribs. Male copulatory organ with tubular atrium and tubular prostate gland.

REMARKS: *Diniatys* has two features which immediately confirm its place in the Haminoeidae: the presence of $1\frac{1}{2}$ whorls only of shell matter, and the three transversely spiny-ribbed gastral plates. It is like *Nipponatys* and *Cylichnatys* in the low profile of the posterior aperture, but is easily distinguished by the presence of the abruptly truncated columella with its tooth-like flange. The number, shape and non-denticulate nature of the lateral teeth recall those of *Nipponatys*, but in that genus the central tooth is smooth. The overall shape of the radular row is close to that in some species of *Haminoea*, but the number of lateral teeth is less than reported in any species. The vertically plicate Hancock's organs also serve to separate *Diniatys* from the genera of this review.

Schepman (1913) placed *Diniatys* (as *Dinia*) in the Scaphandridae as a valid genus, and since then it has been regarded as a subgenus of *Cylichna* in this family by Thiele (1931), Wenz (1959), Maes (1967) and Cernohorsky (1972). It was used as a genus by Pilsbry (1921), Iredale (1929, 1936), Allan (1940) and Habe (1952, 1955, 1961, 1964), whereas Pruvot-Fol (1954) maintained it as a subgenus of *Atys* exactly as propounded by Pilsbry in 1894. A probable synonym of *Diniatys* is the small *Micraenigma* Berry, 1953, whose type species *M. oxystoma* Berry, 1953, from Cedros Island, Baja California is exceedingly like *D. dentifera*.

Two well-known species, *D. dentifera* (A. Adams) and *D. monodonta* (A. Adams) belong to the genus, the former with a wide Indo-Pacific distribution, the latter confined to the western Pacific. A deep-water species, *D. truncatula* (Schepman) is known from 522 m in the Sulu Sea between Borneo and the Philippines. From the Gulf of Suez, *Atys miranda* E. A. Smith was described, and remains unfigured to this day; it was transferred to *Diniatys* by Pilsbry (1894).

Diniatys dentifera (A. Adams, 1850)

Figures 19-25

Bulla (*Atys*) *dentifera* A. Adams, 1850 : 588, pl. 125, fig. 124

Atys dentifera Sowerby, 1868 : fig. 13; Cooke, 1886 : 132; Hedley, 1910:370.

Atys (*Dinia*) *dentifera* H. & A. Adams, 1854:21; Pilsbry, 1894:276, pl. 27, fig. 81; Kobelt, 1896: 27, pl. 8, fig. 15.

Dinia dentifera Schepman, 1913:471.

Diniatys dentifera Allan, 1940:177, fig.; Habe, 1952:141, pl. 20, fig. 12; Habe, 1955:62; Habe, 1961:89, pl. 42, fig. 24; Habe, 1964:136, pl. 42, fig. 24

Cylichna (*Diniatys*) *dentifera* Wenz, 1959:26, fig. 78; Cernohorsky, 1972:209, pl. 59, fig. 7.

Dinia compitorum Pilsbry, 1921:364, fig. 3

Cylichna (*Diniatys*) sp. Maes, 1967:151.

DIAGNOSIS: Shell of $1\frac{1}{2}$ whorls, small to medium size, fairly solid, broadly ovoid to broadly subcylindrical, broadest at mid-length, diameter almost two-thirds length, broadly rounded anteriorly, subtruncate posteriorly. Spiral striae weak to obsolete, strongest anteriorly; axial threads not developed; shell sometimes quite smooth. Aperture broad anteriorly, narrowing posteriorly; inner margin of posterior aperture simply curved, rising obliquely from vertex. Columella short, curved, thickened, labrum not developed; on the inner side a broad thick descending lamina or keel, anteriorly abruptly truncated as a tooth-like projection. Vertex very shallowly concave. Colour transparent with opaque anterior and posterior ends in preserved and fresh shells, opaque white in dead shells.

DIMENSIONS:	Length	Diameter	D/L
Mauritius (N.M.V. F30117)	4.58 mm	2.875 mm	62.7%
Dongara (W.A.M. 1879.69)	3.125	1.96	61.3
	3.0	1.96	65.3
	2.58	1.58	61.3
	2.21	1.42	64.2
Minum Cove (W.A.M. 78.1651)	5.75	3.46	60.1
	3.33	2.17	65.0
	2.67	1.67	62.5

Animal in preservative translucent cream with brown pigment cells scattered in narrow bands in posterior lobes of head and in front of eyes, viscera pinkish-orange. Head broadly subquadrate with sinuate anterior margin and paired posterior lobes folded forward covering eyes. Hancock's

organs large, raised, triangular, with up to 6 irregular, sometimes broken, vertical plicae. Each side of mouth a rounded oral lobe. Foot short and broad, truncate in front and behind, with small parapodia covering anterior part of shell; epipodium filling posterior aperture, not extending beyond shell. Male copulatory organ probably not mature, in lower right wall of head cavity, very small, 420 μm long by 80 μm diameter, with smooth-walled atrium, and prostate gland of granular cells and slender lumen. Nerve ring large, with big cerebral, pleural and pedal ganglia clustered round posterior end of pharynx.

Pharynx large, almost 1 mm long, filling most of head cavity; salivary glands small, clavate, filled with granular cells; oesophagus short and broad, without diverticula. Jaws resembling those of *Weinkauffia*, large, shield-shaped, composed of many rows of oblong brownish elements, 20 μm long, from one narrow edge of which project 9-10 points. Radula with 22 rows of 5.1.5 teeth, central tooth 70 μm wide with three cusps and striated base, lateral teeth smooth, initially hamate becoming awl-shaped and smaller marginally, laterals 2, 4 and 5 have cusp lengths of 65, 45 and 33 μm respectively. Gastral plates 3, haminoeoid in shape, about 400 μm long, strongly curved with up to 20 slightly arcuate transverse ribs, each with a row of points; yellowish-brown in colour with darker brown ribs.

LOCATION OF TYPE: B.M.N.H. Holotype. (Not examined).

TYPE LOCALITY: Lord Hood's Island, now Marutea Atoll, Gambier Islands, French Oceania.

ADDITIONAL MATERIAL EXAMINED: Mauritius, R.F. Geale Colln (N.M.V. F30117, 1 spec.). Dongara, W.A., from gut of *Philineopsis cyanea* (Martens), 24 August 1958, coll. B.R. Wilson (W.A.M. 1879.69, 7 preserved spec.; N.M.V. F30118, 3 preserved and 4 dissected spec.). FOSSIL RECORD: PLEISTOCENE: Minum Cove, Mosman Park, W.A., from top 1 m at W end of fresh rock-fall, 27 February 1966, coll. G.W. Kendrick (W.A.M. 78.1651, 10 spec.).

DISTRIBUTION: Indo-West Pacific: Gulf of Suez, Mauritius, Cocos-Keeling Island, Hawaii, Fiji, Cook Islands, southern islands of Japan, Indonesia, Queensland, Western Australia; Pleistocene to Recent, intertidal to 45 m.

REMARKS: *D. dentifera* is easily separated from *D. monodonta* (A. Adams) and *D. truncatula* (Schepman) by its ovoid shape where the diameter equals about two-thirds the length. The original figure by Adams (? of the Holotype) is of a shell 5.5 mm long by 3.6 mm diameter, with D/L of 66%. There appears to be some variation in shell shape in the figures in the literature, with the posterior lip rising somewhat higher than in the present material. The same and greater variation occurs in the Dongara material which is smaller in size than reported from elsewhere. The specimens are both ovoid and broadly subcylindrical, some have the posterior lip almost level with the body whorl, others have it rising very obliquely or a little higher. In four animals examined from shells of various shapes, no anatomical differences were noted.

The Dongara specimens, 14 in all, were found in the gut of a large specimen of the aglajid *Philineopsis cyanea*, together with specimens of *Haminoea* and *Tornatina*: This predator is well-known for its liking of small bubble-shells.

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STUDIES ON THE REPRODUCTIVE BIOLOGY OF GASTROPODS:
PART 1. THE SYSTEMATIC DISTRIBUTION OF EGG RETENTION IN
THE SUBCLASS PULMONATA (GASTROPODA)

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SUMMARY

Thus far, no pulmonate snail has been unequivocally demonstrated to be viviparous. Most pulmonate snails are oviparous, *i.e.* they release each egg immediately after its formation. On the basis of several years of observations and literature search, a list of known ovoviviparous pulmonates (here defined *sensu lato*, as those animals which retain their eggs instead of releasing them right away) is presented. Ovoviviparity is apparently rare compared with oviparity; it is absent from the entire freshwater order Basommatophora and from all families of slugs. Ovoviviparous reproduction is most common in such families as the Achatinidae, Subulinidae, as well as in several groups of the suborder Orthurethra. On the basis of this survey, it appears that while approximately one-half of the more than sixty families of stylommatophoran families contain at least one ovoviviparous species, the total number of species involved is small.

INTRODUCTION

Reproduction in pulmonate snails — as in other organisms — can be classified into three broad categories: oviparity, viviparity and ovoviviparity. The first term refers to parental organisms which deposit their eggs as soon as they are formed. In the second group, embryos are retained inside the parental organism, which supplies them with nourishment continuously during development. The third group of organisms, called ovoviviparous, retain the eggs inside part of the reproductive tract for some period of time, with the eggs usually hatching inside the parental body, but without having received nourishment other than what was initially contained inside the egg. Among land snails, there are a number of groups such as many Partulidae and Achatinidae which allow the young to hatch inside or carry (retain) the eggs for variable periods of time only to release eggs later, containing advanced embryos. Because of the widespread occurrence of irregularity in the duration of egg retention, the term ovoviviparity is used here to include all those snails which retain eggs from a few days to several weeks, though they eventually hatch either inside the parental body or outside of it. The term "egg retention" may be substituted here for "ovoviviparity".

All animals which are ovoviviparous *sensu strictu* (young hatching from the egg while inside the parent) are egg retainers, but not all egg retainers are ovoviviparous in the strictest sense of the word, only *sensu lato*, as used in this paper. Such a general definition is necessary for the practical consideration of reproductive strategies in land snails and is discussed in greater detail elsewhere (Tompa, in preparation).

The approach for this study was to search for living and preserved specimens containing eggs with advanced embryos. Viviparous snails lay eggs which have not yet undergone even first cleavage (Tompa, personal observations), whereas most ovoviviparous snails will be found to have gastrula and post-gastrula embryos inside their eggs. Therefore, only an ovoviviparous or egg retaining animal will ever be found to contain eggs with advanced young. It is because ovoviviparous animals carry their eggs for many days or weeks that they are often found in the gravid condition. On the other hand, such viviparous snails as *Anguispira*, *Helix*, *Polygyra* and even *Strophocheilus oblongus* with its giant eggs, form each egg within the space of 2-3 hours and lay them at intervals ranging from 15 minutes to 3 hours (unpublished). Since the total duration of egg formation and subsequent deposition in viviparous animals typically takes far less than a single day, these animals will be found in a gravid state only most rarely.

An examination of several thousand preserved museum specimens and field collected animals brought back to the laboratory during the past five years resulted in not a single strictly viviparous snail having been found gravid with eggs, while a high percentage of such ovoviviparous species as *Subulina*, *Achatina* or *Partula* are gravid during the warm seasons. It should be emphasized that ovoviviparous animals often contain not eggs, but young snails which have hatched from eggs while inside the parental uterus. Because these neonates make a first meal of their egg shell remnants immediately after hatching and therefore leave no trace of them in the uterus, animals containing young were often automatically called viviparous in the early literature. However, the definition of viviparity is the provision of continuous nourishment/waste removal to the embryo through some morphological connection, and not a single species of pulmonate snail has been shown to satisfy this criterion. Thus, while by far the largest group of pulmonates are strictly viviparous and a few are ovoviviparous, none can be called viviparous at this time.

The present paper is an attempt to be as comprehensive as possible in listing the rather few cases of demonstrated ovoviviparity (egg retention). The older literature was searched, original descriptions were read and evaluated for accuracy, and the nomenclature was updated (originally almost all land snails were in the genus *Helix*). The only previous attempt at such a compilation was by Pelseneer (1935), but this list is incomplete and the names and systematic positions of the groups as originally presented are now out of date. Originally, I prepared this list for my own use during studies of the evolution of reproduction in gastropods; I present it here in the hope that other malacologists also need such information and will find this a newer starting point for research.

This list is surely not final, but I think one point does emerge clearly, that among pulmonate groups the occurrence of ovoviviparity is irregular and that conspicuously absent from this list are all of the Basommatophora and the various slug families. A similar compilation of reproductive patterns for the remaining Euthyneura and for the Prosobranchia, with an examination of egg morphologies, is in preparation. A

previous paper, which lists the distribution, mineralogy and ultrastructure of stylommatophoran eggs having a calcium carbonate shell, may provide some supplementary information (Tompa, 1976, *J. Morphology* 150; 861-888).

SYSTEMATIC DISTRIBUTION

	Source
CLASS GASTROPODA	
Subclass Pulmonata	
Order Basommatophora — no ovoviviparous (or viviparous species known)	Tompa
Order Stylommatophora	
Suborder Orthurethra	
ACHATINELLIDAE	
Subfamily Pitysiniae	
<i>Celticola</i>	Cooke & Kondo (1960)
<i>Tubuaia</i>	"
Subfamily Lamellideinae	
<i>Lamellidea</i>	"
<i>Tornatellinops</i>	"
Subfamily Tornatellininae	
<i>Elasmias</i>	"
<i>Fernandezia</i>	"
<i>Tornatellina</i>	"
Subfamily Tornatellidinae	
<i>Philopoa</i>	"
<i>Tornatellides</i>	"
Subfamily Achatinellinae	
<i>Achatinella</i>	"
<i>Newcombia</i>	"
<i>Partulina</i>	"
<i>Perdicella</i>	"
Subfamily Tekoulininae	
<i>Tekoulina pricei</i>	Solem (1972)
a) PARTULIDAE	
<i>Eua</i> sp.	Tompa
<i>Partula</i> spp.	Tompa
<i>Samoana</i> spp.	Tompa
b) AMASTRIDAE	
Subfamily Amastrinae	Thiele (1935); Zilch (1959-60)
PYRAMIDULIDAE	
<i>Pyramidula rupestris</i>	Bronn (1912-28); Germain (1930); Taylor (1914); Collier (1889); Tryon & Pilsbry (1885-1937)
VALLONIIDAE	
<i>Pupisoma</i>	Thiele (1935); Gude (1914); Pilsbry (1948)

a) This whole family may be entirely ovoviviparous.

b) The other subfamily, Leptachatiniinae, is entirely oviparous.

- Zoogenetes (Acanthinula) harpa* Steenberg (1925); Pelseneer (1935); Thiele (1935); Tryon & Pilsbry (1885-1937)
- PLEURODISCIDAE
Pleurodiscus balmei Thiele (1935)
 Watson (1920); Tryon & Pilsbry (1885-1937)
- PUPILLIDAE
Lauria cylindracea Steenberg (1925); Zilch (1959-60); Germain (1930); Grasse (1968)
Pupilla cupa Steenberg (1925)
Pupilla muscorum Tompa
Pupilla triplicata Steenberg (1925)
- VERTIGINIDAE
 Subfamily Truncatellinae
Bothriopupa tenvidens "
Pronesopupa (Edentulopupa) admosta "
 Subfamily Nesopupinae — (ovoviviparity may be universal) "
Lyropupa (Mirapupa) perlonga "
Nesopupa (Nesopupilla) plicifera "
Nesopupa (Limbatipupa) newcombi "
- ENIDAE
Rachis (Buliminus) burnayi Pelseneer (1935)
- Suborder Mesurethra
 CLAUSILIIDAE
Balea perversa Pelseneer (1935); Watson (1920); Craven & Smith (1891); Germain (1930)
Clausilia conchinchinensi Pelseneer (1935)
C. similis Pelseneer (1935)
C. (Iphigena) ventricosa Pelseneer (1935); Germain (1930); Loosjes (1941)
Euphaedusa tetsui Loosjes (1941)
Laciniaria (Alinda) biplicata Germain (1930); Loosjes (1941)
L. strauchi Lezhava (1962)
Vestia turgida Husana (1965)
- CORILLIDAE
Corilla Thiele (1935); Gude (1914)
C. erronea Pelseneer (1935)
Plectopylis Thiele (1935); Gude (1914); Tryon & Pilsbry (1885-1937)
- Suborder Sigmurethra
 FERRUSSACIIDAE
Caecilioides acicula Wachtler (1929)
C. consobrina Tompa
C. gundlachi Tompa

c) Likehachev and Rammelmeier consider the Vertiginidae to be a family of the Pupillidae; they call the former group viviparous. Grasse calls the family Vertiginidae generally oviparous.

<i>Ferrussacia follicula</i>	Pelseneer (1935); Germain (1930); Watson (1928)
<i>F. (Glandina) lamellifera</i>	Pelseneer (1935)
<i>F. oranensis</i>	Pelseneer (1935); Watson (1928)
<i>F. (Glandina) procerula</i>	Pelseneer (1935)

STREPTAXIDAE

<i>Ennea</i>	Gude (1914)
<i>Streptaxis burmanius</i>	Pelseneer (1935)
<i>Streptaxis obtusus</i>	Pelseneer (1935)
<i>Streptostele crassicostata</i>	Pelseneer (1935)
<i>S. crassicrenulata</i>	Tompa
<i>S. horei</i>	Venmans (1955)

SPIRAXIDAE

<i>Spiraxis terebella</i>	Tompa
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d ACHATINIDAE

<i>Achatina alabaster</i>	Pelseneer (1935)
<i>A. crawfordi</i>	Pelseneer (1935); Clapp (1897)
<i>A. erronea</i>	Pelseneer (1935)
<i>A. flammea</i>	Pelseneer (1935)
<i>A. panthera</i>	Pelseneer (1935)
<i>A. zebra</i>	Pelseneer (1935)
<i>Burtoa nilotica</i>	Reynell (1906); (but see Owiny, 1974)
<i>Cochlitoma</i>	Standen (1917)
<i>Liguus</i>	Standen (1917)
<i>Limicolaria martensiana</i>	Owiny (1974)
<i>L. smithi</i>	Robson (1912)

d SUBULINIDAE

<i>Glessula</i>	Standen (1917)
<i>Homorus mambocansi</i>	Pelseneer (1935)
<i>Leptinaria</i> spp.	Pelseneer (1935)
<i>Neoglessula vivipar</i>	Zilch (1959-60)
<i>Obeliscus</i>	Zilch (1959-60)
<i>Obeliscus obeliscus</i>	Spence (1919)
<i>Opeas</i>	Zilch (1959-60)
<i>Opeas dominicensis</i>	Pelseneer (1935)
<i>Opeas viviparus</i>	Pelseneer (1935)
<i>Pseudoglessula libera</i>	Solem & van Bruggen (1976)
<i>Rhodea</i>	Zilch (1959-60)
<i>Rumina decollata</i>	Pelseneer (1935)
<i>Stenogyra</i> spp.	Pelseneer (1935)
<i>Subulina kassaiana</i>	Venmans & Fromming (1957)
<i>S. octona</i>	Owiny (1974)
<i>Zootecus</i>	Zilch (1959-60)

RHYTIDIDAE (PARYPHANTIDAE)

<i>Delos (Rhenea) coresia</i>	Kondo (1943)
<i>Delos (Rhenea) voganus</i>	Pelseneer (1935)
<i>Ouagapia</i>	Zilch (1959-60)
<i>Ouagapia gradata</i>	Kondo (1943)

d) Ovoviviparity is most common in this family and may be viewed as the dominant type of reproduction.

<i>Ouagapia oualaniensis</i>	Kondo (1943)
<i>Ouagapia rapida</i>	Kondo (1943)
<i>Ouagapia ratusukuni</i>	Kondo (1943)
<i>Prioniscus</i>	Thiele (1935)
<i>Rhytida aequalis</i>	Pelseneer (1935)
<i>R. (Ptychorhytida) inaequalis</i>	Kondo (1943); Pelseneer (1935)
ACAVIDAE	
<i>Stylodon</i> sp.	Zilch (1959-60); Tryon & Pilsbry (1885-1937)
<i>Stylodon studeriana</i>	Bronn (1912-28)
<i>Stylodon unidentata</i>	Bronn (1912-28)
HAPLOTREMATIDAE	
<i>Haplotrema (Anisotrema) sportella</i>	Thiele (1935)
^e <i>Zophos voganus</i>	Baker (1930)
	Pelseneer (1935)
UROCOPTIDAE	
<i>Apoma</i>	Zilch (1959-60)
<i>Brachypodella agnesiana</i>	Spence (1916)
<i>B. chemnitzia</i>	Spence (1916)
<i>B. gracilis</i>	Spence (1916)
<i>B. obesa</i>	Spence (1916); Clapp (1915)
<i>B. suturalis</i>	Spence (1916); Clapp (1915)
ENDODONTIDAE	
^f _g <i>Helicodiscus parallelus</i>	Tompa; Gugler (1972)
VITRINIDAE	
^h <i>Vitrina</i> sp.	Pelseneer (1935)
EUCONULIDAE	
<i>Guppya gundlachi</i>	Baker (1925)
<i>Guppya (Conulus) vacans</i>	Pelseneer (1935)
<i>Lamprocystis</i>	Thiele (1935)
<i>Microcystis myops</i>	Pelseneer (1935); Grasse (1968)
	(subfamily ovoviviparous)
<i>Sitalina</i>	Thiele (1935)
^j ARIOPHANTIDAE	
<i>Lousia</i>	Thiele (1935)
<i>Pachystyla inversicolor</i>	Pelseneer (1935)

e) Grasse calls this a streptaxid of the subfamily Zophinae; I have followed Zilch's assignment by placing it in the Haplotrematidae merely for convenience, as I am not familiar with this group's affinities.

f) Some place this genus in its own family, the Helicodiscidae; I have again followed Zilch for the convenience of keeping everything according to one system, unless obviously incorrect. This genus, *Helicodiscus*, appears to be a closely related group, entirely ovoviviparous.

g) The endodontid *Anguispira kochi*, reported to be viviparous by Gugler (C. Gugler, 1973, Amer. Malac. Un. Bull. 38; 10) is definitely oviparous. I have personally examined this snail and have bred it in my laboratory. No doubt, what Gugler examined was an *Oreohelix*.

h) This record is questionable and because of its singular report from an entire family it ought to be re-examined before being accepted with certainty. Nevertheless, I include it in this list to call it to attention.

j) The affinities of these genera are not clear to me; Zilch includes them in the family Ariophantidae whereas Thiele calls them members of the Helicarionidae.

SYSTROPHIIDAE (SCOLODONTIDAE)

<i>Miradiscops variolata</i>	Baker (1925)
<i>Scolodonta cayennensis</i>	Baker (1925)
<i>S. eudiscus</i>	Tompa
<i>S. thomasi</i>	Tompa
<i>Tamayoa trinitaria</i>	Baker (1925)

SAGDIDAE

<i>Hojeda</i>	Thiele (1935)
<i>H. peraffinis</i>	Tryon & Pilsbry (1885-1937)
<i>H. vortex</i>	Tryon & Pilsbry (1885-1937)
<i>Sagda haldeniana</i>	Pelseneer (1935)
<i>Zaphysemia</i>	Pelseneer (1935)
<i>Z. tenerrima</i>	Tryon & Pilsbry (1885-1937)

OREOHELICIDAE

^k <i>Oreohelix</i>	Pilsbry (1948)
<i>O. strigosa</i>	Bavay (1884)
<i>O. vortex</i>	Solem (1975)
<i>O. waltoni</i>	Solem (1975)
<i>Radiocentrum</i>	Zilch (1959-60)

BRADYBAENIDAE

^h <i>Euhadra luchuana</i>	Pelseneer (1935)
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HELICIDAE

^h <i>Theba cartusiana</i>	Hopwood (1944)
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UROCYCLIDAE

<i>Trochozonites ibuensis</i>	Lamy (1929)
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k) Zilch is incorrect in considering the subgenus *Oreohelix* to be oviparous and the other related subgenus of *Oreohelix* (*sensu lato*). *Radiocentrum*. to be ovoviviparous; the facts are *vice versa*.

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A NEW SPECIES OF THE GENUS *GLACIDORBIS* (?HYDROBIIDAE: GASTROPODA) FROM GREAT LAKE, TASMANIA.

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SUMMARY

A new species of operculate snail, *Glacidorbis pawpela* sp. nov., is described from Great Lake, Central Tasmania. More distributional data is given for the other two Australian members of the genus.

INTRODUCTION

Following recent work on the two Australian species, *Glacidorbis hedleyi* and *Glacidorbis pedderi*, by Meier-Brook and Smith (1975), further distributional data have been sought to establish the range of these species. Field ecologists from state instrumentalities and universities have provided valuable data for this study. As part of this cooperation Mr. Wayne Fulton from the Inland Fisheries Commission, Tasmania submitted what he regarded as unusual specimens from Great Lake for identification. These were recognised as a large new species of *Glacidorbis*, and through the ready cooperation of the Inland Fisheries Commission, sufficient additional material was collected to enable the species to be described.

DESCRIPTION

Glacidorbis pawpela sp. nov.

Figures 1-6

DIAGNOSIS: A species of *Glacidorbis* with a long, wide mesocone on the rhachidian bearing 16 to 20 denticles on each side; shell smooth, rounded with no carination present, more than 1 mm in diameter at 2½-3 whorls.

DESCRIPTION: Shell planispiral, thin, fragile, 2½-3 whorls, rounded with no keel or carinations present, often with obvious growth lines (Fig. 3). Diameter of whorls increases sharply with growth. Shell diameter is greater than 3 mm at the 2½ whorl stage. Fine brown periostracum present, usually covered by brown crystalline deposit. Operculum thin, horny, paucispiral (Fig. 4).

The radula consists of 22-26 rows each represented by a single rhachidian. The rhachidian is a large triangular recurved mesocone with a row of 17 to 18 denticles along each postero-lateral margin (Fig. 5 & 6). Each rhachidian is a heavy structure shaped like a reptilian jaw, with a curved anterior rounded keel, a sharp pointed cusp and a wide triangular winged base plate with articulating surfaces with adjacent teeth. The denticles are flattened peg-like structures with inward curving pointed ends. The posterior surface of the rhachidian, inside the rows of denticles, is concave to allow the rounded keel surface of the next tooth to fit into the concavity. No lateral teeth are present.

Two preserved animals were dissected, a female with a shell of 3 whorls and a maximum diameter of 4.4 mm, and a male with broken shell of 2½ whorls. The female had two large embryos in the lower uterus (Fig. 1a). The largest of these had a shell of ¾ whorl, maximum diameter 1.3 mm, minimum diameter 1.0 mm; the other was about half this size. A further three very small embryos were seen in the upper part of the reproductive tract. Few details of the anatomy were revealed from these two specimens because of their small size.

Externally the head and operculum is very similar to *G. pedderi*. The eyes are situated at the base of short round tentacles, the head and foot have a distinct bilobed appearance with the concave, paucispiral operculum being attached to the rear of the foot with about a third of its length being free, protruding forward.

An examination of the pallial cavity reveals no ctenidia present. The pallial cavity opens to the exterior on the right side, the ventral and median sides of the opening being a raised, thickened band of tissue. This passes backwards on the floor of the pallial cavity, like a flagellum that has fused to the surface.

The buccal mass is short with the oesophagus emerging from the dorso-posterior end. A loose nerve ring also appears to be situated at the posterior end of the buccal mass, around the oesophagus, with pedal ganglia below the pedal gland, free in the ventral part of the body cavity. Arising from the point of insertion of the oesophagus into the buccal mass are two short ducts with long white sausage-shaped salivary glands at least twice the length of the buccal mass. The long oesophagus, without expansion into a crop, leads to a small stomach partly embedded in the digestive gland.

Sexes appear to be separate in the species, the specimen with large embryos in the uterus having no sign of a penis. The male had what appeared to be an everted penis emerging from a damaged left side of the head (Fig. 1b). This took the form of a short, straight, finger-like process which appeared to be soft and hollow with longitudinal rows of fine papillae. Around the base of this was a wide, coiled, collar-like structure about twice the diameter of the papillate process. This collar was separated from the process by a deep groove and bore fine longitudinal folds. Distal to the collar the structure was attached to an anterior duct of the reproductive tract by a short narrow process.

TYPE MATERIAL: Holotype in the Tasmanian Museum, E10389, a complete specimen with animal preserved in 70% alcohol (shell slightly damaged).

Nine paratypes; eight complete with animals preserved in 70% alcohol and one dry, prepared for SEM examination. Paratype 1 lodged in Tasmanian Museum, E10390; paratypes 2-8 in National Museum of Victoria, F30145 a-g; paratype 9 in National Museum of Victoria, F30146, mounted for SEM (Fig. 3).

DIMENSIONS:

Holotype	E10389	Max. 3.6 mm	Min. 3.0 mm	Whorls 2-3/4
Paratype 1	E10390	" 2.7 mm	" 2.2 mm	" 2
2	F30145a	" 2.2 mm	" 1.6 mm	" 1-1/2
3	F30145b	" 3.0 mm	" 2.5 mm	" 2-1/2
4	F30145c	" 3.7 mm	" 3.1 mm	" 2-3/4
5	F30145d	" 3.0 mm	" 2.5 mm	" 2-1/4
6	F30145e	" 2.5 mm	" 1.9 mm	" 1-3/4
7	F30145f	" 2.4 mm	" 1.9 mm	" 1-1/2
8	F30145g	" 2.5 mm	" 2.0 mm	" 1-3/4
9	F30146	" 3.5 mm	" 2.9 mm	" 2-1/2

TYPE LOCALITY: Elizabeth Bay, Great Lake, Tasmania, from a soft mud bottom at 30 m depth, water temperature <4°C. The holotype and paratypes 2 and 9 were collected by W. Fulton, 7 November, 1975; the remaining paratypes were collected by W. Fulton and B.J. Smith, 1 September, 1978.

OTHER MATERIAL: Three other specimens were collected with the type series on 1 September 1978. These were used in dissection and the remains are lodged in the National Museum of Victoria (F30147).

REMARKS: *Glacidorbis pawpela* differs from all other members of the genus by the size of the shell and the structure of the rhachidian. The other three known species, *G. pedderi* from

Tasmania, *G. hedleyi* from Victoria and New South Wales and *G. magallanicus* from south Chile, all have a shell diameter under 3 mm for a $2\frac{1}{2}$ whorl shell and the rhachidian mesocone bears eight or less denticles on each side. *G. pawpela* has a shell diameter greater than 3 mm for a $2\frac{1}{2}$ whorl shell and the rhachidian mesocone bears 16 to 20 denticles on each side.

Great Lake is an oligotrophic lake with fresh, slightly acidic waters. Species associated with *G. pawpela* are the bivalve *Sphaerium* (*Musculium*) *tasmanicum*, three or four species of oligochaetes, chironomid fly larvae and the phreatoicid *Oncholaelson spatulatus* (W. Fulton - pers. comm.). The specimens were collected by Ekman-Birge grab. Several dead shells of *G. pawpela* were collected in the same sample series. On examination, these were found to consist of the periostracum only, all the calcareous elements of the shell having been broken down. This suggests that live snails have a dynamic mechanism for retaining the calcareous elements of the shells in conditions where the chemical conditions of the environment would cause these structures to break down.

The presence of large, developing embryos in the uterus is of interest as viviparity has also been noted in two of the other three members of the genus (Smith - unpublished, Meier-Brook and Smith, 1975).

ETYMOLOGY: *pawpela* is a Tasmanian Aboriginal word, used by tribes from Oyster Bay to Pittwater (Roth, 1899), meaning "large or big". This name seems appropriate for a Tasmanian species that is the largest of the genus, coming from Great Lake, the largest lake in Tasmania.

OTHER GLACIDORBIS SPECIES

Further distributional and ecological data have become available on the two other Australian species of *Glacidorbis*. These have emerged as a result of ecological survey work by staff and students of Monash University, Victoria and the University of Tasmania. The present known distribution of the Australian species of *Glacidorbis* is shown in Fig. 2.

Glacidorbis pedderi (Smith, 1973) is known from four localities in western Tasmania. The original specimens of this species were collected from Lakes Pedder and Edgar prior to their inundation in the enlarged Lake Pedder. No further specimens have been found in this locality. However teams of staff and students from the University of Tasmania have found it in three other localities during wide ranging limnological surveys in that state. It was taken on submerged logs, from *Triglochin* and from aquatic plants in a small perched lake just upstream from Butler's Island in the Lower Gordon River, Western Tasmania on 25 January 1976 by P.S. Lake, A. Richardson, D. Coleman and P. Allbrook. The water was reported as brown and acidic. A specimen was taken by T. Walker from a lagoon at Cleveland, Western Tasmania on 26 August 1974 and several specimens by A. Richardson et al at the Dip River falls, north western Tasmania on 28 January 1974. These scattered distribution records imply that the species is probably widespread throughout western Tasmania in cold acidic waters. Despite this additional material coming to light, little more can be added to the knowledge of the anatomy of the species. So far no direct evidence has emerged of viviparity in this species though this can be surmised as the other three species have all been shown to be viviparous.

Glacidorbis hedleyi Iredale, 1943 is now known from seven localities in the Great Dividing Range of central and eastern Victoria and southern New South Wales (Smith, 1978).

These localities are:—

- (a) Running Creek, above and below Mason Falls, Kinglake National Park, Victoria (600 m), April 1977 in shallow water on stones by A. Fletcher.
- (b) Backwater of Acheron River, between Warburton and Narbethong, Victoria (900 m), in July 1975 in organic debris by L. Macmillan, R. Plant and B. J. Smith.
- (c) *Sphagnum* bog at summit of Mt. Baw Baw, Victoria (1500 m), in February and April 1976 in shallow acidic water by J. McAuley.
- (d) Mt. Buffalo National Park, Victoria (1700 m), in a tributary of Buffalo Creek (Wirbill Plain) in April 1978 in gravel by A. Fletcher and in stream from *Sphagnum* bog in acidic water in Dingo Dell in January 1978 by B. J. Smith.
- (e) Cape Creek, Bogong High Plains, Victoria (1500 m) in February, 1978 in shallow acidic water on gravel by A. Fletcher.
- (f) In small creek near junction of Native Cat Track and Nunning Track, Cobbras, East of Benambra, Victoria (1200 m) in January 1976 under stones in shallow water by R. Plant.
- (g) Blue Lake, Kosciusko National Park, Mt. Kosciusko. New South Wales (1700 m) — type locality.

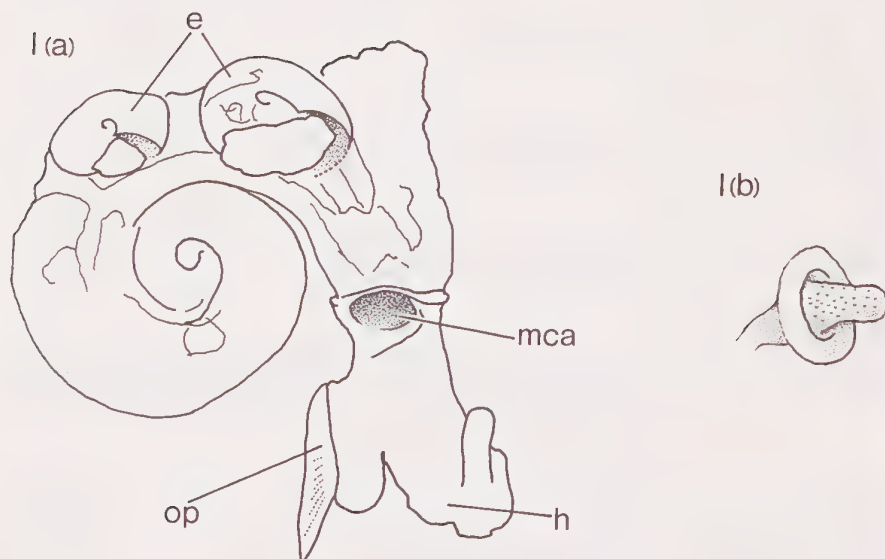


FIGURE 1. Diagrams of the animal of *Glacidorbis pawpela* sp. nov. showing (a) position of the embryos in the uterus (e — embryos, h — head, mca — mantle cavity aperture, op — operculum); (b) shape of the penis.



FIGURE 2. Map showing the distribution of *Glacidorbis hedleyi* (solid dots); *Glacidorbis pedderi* (circles); *Glacidorbis pawpela* sp. nov. (star).



FIGURES 3-6.

3. Dorsal view of shell of *Glacidorbis pawpela* sp. nov. paratype No. 9. (NMV F30146) (X22).

4. Ventral surface of operculum of *Glacidorbis pawpela* sp. nov. (X 40).

5. & 6. Radula of *Glacidorbis pawpela* sp. nov. showing large rhachidian (Fig. 5 X800; Fig. 6. X1000).

All these localities are in forest or alpine areas and have high quality, slightly acidic waters with decaying vegetable matter found associated with the *Glacidorbis* populations. The water is cold for most of the year with the localities subject to snow every winter. It is assumed that the species occurs throughout the Great Divide region of central and eastern Victoria and southern New South Wales. More detailed ecological work is to be carried out on this species.

Several specimens of *Glacidorbis hedleyi* have been found to contain large, well developed embryos in the uterus, some up to 3/4 whorl showing that viviparity occurs in this species.

DISCUSSION

The discovery of a third species of *Glacidorbis* in south-eastern Australia from a bay of Great Lake on the Central Plateau of Tasmania throws more light on this interesting group of freshwater operculates. Despite an extensive ecological survey of Great Lake (W. Fulton — pers. comm.) the new species is only known from Elizabeth Bay, half way up the eastern side of the Lake. Here it appears to be fairly common with 10 live specimens being taken from seven 0.1 m grab samples taken from two spots about 80 m apart in the centre of the bay. Before the water level of Great Lake was artificially raised in the 1930's, Elizabeth Bay was probably a separate lake only being joined in times of very high inflow. The bay is still a shallow basin with a submerged sill between it and the main body of the lake.

Little plant material was collected with the specimens, the soft mud and turbid water making plant growth impossible. Large numbers of freshwater oligochaetes were found with the snails and it is surmised that small specimens of these animals probably form the main food for the *Glacidorbis*. It is not known how the solid, jaw-like teeth are used in feeding but one might expect them to be used in conjunction with ancillary food holding structures to enable the teeth to shred and transport the food.

The value of the up-surge in interest in the environment, and particularly in the ecology of freshwater biological associations in both Tasmania and Victoria by local universities, is underlined by the results presented here. These ecological surveys have brought to light a great deal of valuable data only obtainable by the detailed, painstaking collecting now being undertaken in many almost inaccessible localities in the two states. Much more of this work needs to be done to fill in the much needed distributional and ecological details still wanting for many of our native animals.

These surveys have reinforced the earlier impression that the species of *Glacidorbis* prefer oligotrophic conditions of fresh, slightly acidic waters which remain cold for most of the year. All the localities where they have been found are subject to winter snow and almost constant cold conditions.

The family placement of *Glacidorbis* is still not resolved, though by elimination it is reasonable to place it close to the Hydrobiidae. Hydrobiids show a wide radiation in southern Australia and the presence of small planispiral hydrobiids in the oligotrophic waters of the mountain systems, showing convergence with the small planispiral planorbids, would be no surprise. The strange radula can possibly be derived by gross enlargement of the hydrobiid triangular rhachidian in response to an unusual feeding habit. However, it is obviously so far removed from any other known Australian hydrobiid as to keep its relationship in doubt till more information is forthcoming.

Now more material of the species has come to hand and several fairly easily accessible habitats located, a more intensive ecological and morphological study is planned.

ACKNOWLEDGEMENTS

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NEW LOCALITY RECORDS FOR *LOPHOPLEURELLA WILSONI* (TATE, 1889)
(OPISTHOBRANCHIA : SACOGLOSSA) FROM SOUTHERN AUSTRALIA.

Robert Burn Hon. Associate, National Museum of Victoria, Melbourne.

For 78 years from its discovery among algae dredged just within Port Phillip Heads, Victoria by J. Bracebridge Wilson in the summer of 1888 (Wilson, 1890 : 64), the holotype of *Lophopleurella wilsoni* (Tate, 1889 : 66) was the only known specimen. The type specimen is now housed in the South Australian Museum, Adelaide.

In 1966, the writer twice reported the species from intertidal areas near to the type locality (Burn, 1966b : 270) and described and figured the living animal and its anatomy (Burn, 1966a : 58). An additional specimen from Flinders Ocean Beach, Victoria was noted (Burn, 1969 : 80), followed soon after by some brief comments on the species (Burn, 1972 : 177). Since then the species has been found a number of times at the same and other Victorian localities, extending the range eastward to San Remo, at the eastern entrance to Westernport.

At the time of the 1972 paper, all data suggested that *L. wilsoni* had a very restricted distribution along the central coastline of Victoria. However, during 1978 and the summer of 1979, a number of specimens were collected at localities on the eastern and western coasts of South Australia, indicating a far greater range for the species than anticipated.

Data for the new Victorian and South Australian records follow:

San Remo jetty, Westernport, Victoria, from *Caulerpa*, August 1978, coll. Ian Kirwen, 1 specimen live length 11 mm (F30123). Alive, body yellowish-green with a very pale cream anastomosing network, rhinophores with orange tip, broad parapodial lobes with orange tip and subapical pale blue band.

Flinders Ocean Beach, Westernport, Victoria, from *Caulerpa sedoides* on rock platform, March 1976, coll. Ian Kirwen, 5 specimens, largest preserved 7 mm long (F30125). Alive, body yellowish-green with darker green anastomosing network, rhinophoral tips paler green, rolled parapodial lobes with orange tip above a white band tending to be blue-tinted below, narrow blue margins to basal half of lobes.

American River, Kangaroo Island, South Australia, 2 m on seagrass, 10 March 1978, coll. Neville Coleman, 2 specimens, larger preserved 9 mm long (F30124). Alive, body green with darker green heavy anastomosing network, rhinophores similar to body, rolled parapodial lobes with faint orange tip above a bluish-white band and light blue margins.

Rapid Bay jetty, St. Vincent Gulf, South Australia, on *Caulerpa trifaria*, April 1978, coll. Ian Kirwen, 4 specimens, largest live length 11 mm (F30122). Alive, body pale yellowish-green with darker green anastomosing network, rhinophores similar to body, parapodial lobes only partially rolled, faint orange tip above white band, blue margins to basal part of lobes.

East of Pt. Sinclair, western South Australia, from green algae, January 1979, coll. David Howlett, 1 specimen preserved length 7 mm (F30120).

Pt. Sinclair jetty, western South Australia, from green algae, January 1979, 1 specimen preserved length 5 mm (F30121).

Colour variation in this material is not great. The body may be pale green or darker, with lighter or darker network. Orange pigment may be present on the tips of the rhinophores and parapodial lobes, and may be prominent or indistinct. The white band below the tip of the parapodial lobes may be present or absent, if present may be tinted with blue in the lower portion. The blue margins of the parapodial lobes may be continuous and distinct, or confined to the basal half and indistinct, or absent. The animal and shell are identical throughout the range.

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NEW SPECIES OF *ATHLETA (TERNIVOLUTA)* AND *NANNAMORIA*
(MOLLUSCA : VOLUTIDAE) FROM THE CAPRICORN CHANNEL,
CENTRAL QUEENSLAND, AUSTRALIA.

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SUMMARY

Athleta (Ternivoluta) insperata, sp. nov. and *Nannamoria inopinata* sp. nov. are described from 168-365 m in the Capricorn Channel of central Queensland, Australia. The former is closely related to the Late Miocene *A. (T.) bungae* Darragh and the latter to the Middle Miocene *N. limbata* (Tate) from the Tertiary of south-eastern Australia.

INTRODUCTION

The occurrence in Australia of deeper water volute species closely related to common Tertiary fossil volutes is now reasonably well documented. (Darragh, 1971; Wilson, 1972). Genera, such as *Livonia*, *Ericusa*, *Notopeplum*, *Nannamoria*, *Notovoluta* and *Athleta (Ternivoluta)*, are widely distributed in the fossil record and they are the dominant element in the volute fauna of the present day, particularly in the cool to warm temperate waters of the continental shelf of the southern half of the continent. It is, therefore, not surprising that dredging in the deep waters of the Capricorn Channel has yielded further examples of such species.

The 1977 *Kimbla* cruise through the Capricorn Group by the Australian Museum has resulted in the extension northward of many records of southern species and, in addition, brought to light hitherto undescribed material. Through the kindness of Dr. Winston Ponder, Curator of Molluscs, Australian Museum, Sydney, the writer has been permitted to examine and report on the volute material from this expedition.

There are two new volute species to hand at present and it is anticipated that other species will come to light in the future. The first is a species of *Athleta (Ternivoluta)*, closely related to *A. (T.) bungae* Darragh from the late Miocene of Gippsland, Victoria. Hitherto, this subgenus, though known from many species in the fossil record (Darragh, 1971), has been represented in the living fauna by a single species *A. (T.) studeri* (Martens), the type of the genus. The latter species has a restricted distribution in deep water (100 - 180 m) off Southern Queensland and Northern New South Wales.

The other taxon is a species of *Nannamoria*, very closely related to *N. limbata* (Tate) from the Middle Miocene of Central and Western Victoria. *Nannamoria* (= *Paramoria*)

is represented by four living species which range from the Central West Coast of Western Australia around to Southern Queensland. These species are *N. capricornea* (Wilson), *N. guntheri* (Smith), *N. amacula* Iredale and *N. parabola* Garrard. The occurrence of this new species extends the range of the genus to Central Queensland and about as far north on the east coast of Australia as on the west coast. It should be noted here that the writer does not consider that there are sufficient grounds for separating *Paramoria* [McMichael], 1960 (Type species, *Voluta guntheri* Smith) from *Nannamoria* and that *N. capricornea*, originally placed in *Volutocornus*, but correctly compared by Wilson (1972) with the Miocene fossils, *N. ralphi* and *N. limbata*, is regarded by the writer as a *Nannamoria*. The reasons for these assignments will be given in more detail in another place.

SYSTEMATIC DESCRIPTIONS

Athleta (*Ternivoluta*) Martens, 1897

Athleta (*Ternivoluta*). Darragh, 1971, p. 170 (with detailed description and synonymy)

The writer (Darragh, 1971) has revised the taxa in this subgenus in some detail and also has commented on relationships of other generic taxa in the subfamily. Rehder (1974) has questioned some of the writer's proposals, based on his belief that the columella folds within the subfamily are of major systematic importance at the generic level. It is not the intention here to enter into a detailed critique of Rehder's proposals except where they have a bearing on the material in hand, however, the writer does not believe that columella plaits can be used reliably as Rehder has done.

Rehder prefers to accept *Volutocorbis* Dall, 1890 as a genus in its own right, distinct from *Athleta*, and places *Ternivoluta* as a subgenus of *Volutocorbis*. Whether one considers *Athleta* and *Volutocorbis* as separate genera or not, is a matter of opinion, and the writer prefers to adhere to his original opinion that they are not separate taxa. If *Volutocorbis* is accepted, it can only be used for the group of Paleocene cancellate species in North America. The European Eocene and South African living cancellate species are homeomorphs and are not directly related to the type species of *Volutocorbis*, *V. limopsis*. As the writer has already noted (Darragh, 1971), cancellate sculpture can and does arise many times in separate lineages within the Tertiary in this subfamily, including the Australian representatives. The writer has made it clear that the living *Ternivoluta stuederi* and the Australian Tertiary species are part of the one lineage and must all be placed in the same generic taxon, not as Rehder suggests, the Tertiary species in *Volutocorbis* and the single living species in *Ternivoluta*. Contrary to Rehder's statement, the Tertiary species have an identical protoconch to the living as the writer has stated and illustrated (Darragh, 1971, p. 170, Fig. B, C). The columella pad that Rehder states is not present in the Tertiary species and is present in living *Ternivoluta* is a variable feature. It is often present on specimens of the Tertiary species and it is often absent. Certainly it is variable feature on specimens within the same species and seems to be present on the more mature specimens in the population. Its presence or absence can have no generic or specific significance in this instance. The discovery of a new living species of *Ternivoluta*, closely related to the late Miocene *A. (T.) bungae* further strengthens the writer's argument.

FIGURES 1-11.

- 1, 6 *Nannamoria inopinata* sp. nov., C 108644 a, holotype, 42 km N.E. of Lady Musgrave Is., Qld., x 1.25.
2. *Nannamoria inopinata* sp. nov., C 108644 b, paratype, 42 km N.E. of Lady Musgrave Is., Qld., x 1.3.
- 3, 5. *Nannamoria inopinata* sp. nov., C 109012, paratype, 39 km E. of Lady Musgrave Is., Qld., x 1.5.
- 4, 7. *Athleta* (*Ternivoluta*) *insperata* sp. nov., C 108686 b, paratype, E. of North West Is., Qld., x 2.
- 8-9. *Athleta* (*Ternivoluta*) *insperata* sp. nov., C 109017, holotype, 30 km off North Reef, Qld., x 2.
- 10-11. *Athleta* (*Ternivoluta*) *insperata* sp. nov., C 108686 a, paratype, E. of North West Is., Qld., x 1.7.

All specimens coated with ammonium chloride except in figures 6 and 9.



1



2



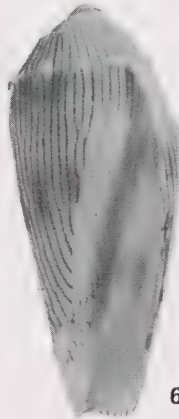
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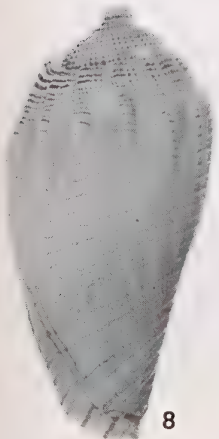
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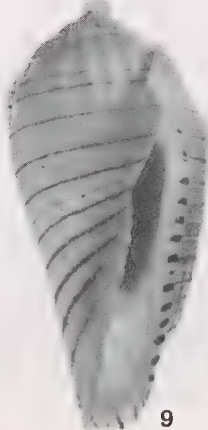
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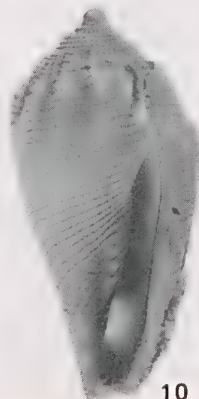
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10



11



FIGURE 12. *Nannamoria inopinata* sp. nov., C 108644 a, radula of holotype.

Athleta (Ternivoluta) insperata sp. nov.

Figures 4, 7–11

DESCRIPTION: Shell pyriform with a domelike to subconical spire and rounded bodywhorl tapering gently to the anterior canal. Protoconch prominent, smooth, large (2.2 mm) of $1\frac{1}{2}$ whorls, the first whorl of which is globose and deviated at right angles to the axis of the shell; second half whorl merging abruptly with the spire whorls. Posterior whorl slope of spire without sutural groove and somewhat convex, producing an almost domeshaped spire. Posterior whorl slope of body whorl convex; anterior whorl slope convex posteriorly then tapering gently to the anterior. Shoulder of body whorl very weakly, if at all, developed. Sculpture on spire cancellate, consisting of fine subequal lirae and axial costae, nodulate at their intersection. Body whorl with more prominent spiral lirae; axial sculpture weak except near the shoulder where it forms short, thick plicae which are raised into slight nodes where crossed by the spiral lirae. Columella with two or three major plaits and many minor plaits on a thick raised columella pad.

Colour of shell, light fawn to cream with thin spiral chestnut lines.

Animal with a broad flat foot; operculum and siphonal appendages absent; eyes on prominent stalks. Head divided by a prominent median cleft and laterally produced into two tentacles behind which are situated the eye stalks. Tubular salivary gland of anterior digestive system very long and separated from the racemose salivary gland. Gland of Leiblin arising from the oesophagus well behind the oesophageal nerve ring.

DIMENSIONS: Holotype C 109017	L 31	HA 26	W 16
Paratype C 108686 a	L 33	HA 25	W 17
Paratype C 108686 b	L 27	HA 21	W 14

LOCATION OF TYPES: Australian Museum, Sydney.

Holotype C 109017, collected P. Colman and F. Rowe, 18 Nov. 1977.

Paratypes C 108686 a, b, collected W.F. Ponder and I. Loch, 14 Dec. 1977.

TYPE LOCALITY: 30 km off North Reef, Capricorn Group, Queensland. $23^{\circ} 11.5'S$, $152^{\circ} 14.5'E$. 188 m, thick, grey mud. 1977 *Kimbla* Cruise Station 4.

OCCURRENCE: 40 km E. of Lady Musgrave Is., Queensland. $24^{\circ} 44'S$, $152^{\circ} 49'E$, 348–357 m, shelly grey ooze. 1977 *Kimbla* Cruise Station 2, 17 Nov. 1977. 39 km E. of Lady Musgrave Is., Queensland. $23^{\circ} 33.7'S$, $152^{\circ} 37'E$. 348–339 m. 1977 *Kimbla* Cruise Station 3, 17 Nov. 1977. East of North West Is., Capricorn Channel, Queensland. $23^{\circ} 19.5'S$, $152^{\circ} 35.4'E$. 320 m globigerina mud. 1977 *Kimbla* Cruise Station 23, 14 Dec. 1977. 42 km N.E. of Lady Musgrave Is., Queensland. $23^{\circ} 38.8'S$, $152^{\circ} 45.5'E$, 365 m. 1977 *Kimbla* Cruise Station 24, 14 Dec. 1977.

MATERIAL: Types, seven adult and four juvenile specimens and seven fragments.

COMMENTS: This species most closely resembles the Late Miocene *Athleta (Ternivoluta) bungae* Darragh from Gippsland, Victoria, from which it is probably descended. It is, however, approximately half the size of that species, has a dome-like rather than conical spire, has more prominent shoulder nodules on the body whorl and the sculpture of the spire is much finer and more evenly cancellate. The other living species of the subgenus *A. (T.) studei* Martens, differs in having a prominent shoulder and is almost devoid of axial or spiral sculpture. None of the other species of the subgenus has any close resemblance.

The gross morphology of the animal is very similar to that of *Athleta (A.) abyssicola* from southern Africa (Woodward, 1900). The radula was not able to be examined. A specimen of *A. (Ternivoluta) studei* (Australian Museum C 63142) was examined externally and this had a head with a prominent median cleft, eyes on long stalks and lacked siphonal appendages as in the above species.

The colour pattern is similar to that preserved on specimens of *Athleta (A.) spinosa* (Linnaeus) from Grignon (Mid. Eocene) in the Paris Basin.

Nannamoria Iredale, 1929

Nannamoria Iredale, 1929 *Rec. Aust. Mus.* 17(4): 181. (Type species: *Nannamoria amicula* Iredale).

Nannamoria inopinata sp. nov.

Figures 1-3, 5-6, 12

DESCRIPTION: Shell biconic to subcylindrical with a short blunt almost dome-like spire. Protoconch of three dome-like whorls, coiled in the axis of the spire. Spire whorls convex, partly concealed by the overlapping of succeeding whorls and occasionally bearing small spinose nodules at the anterior suture. Body whorl gently convex and tapering anteriorly, bearing at the posterior quarter a row of 8-10 blunt to subspinose nodules. Spiral and axial sculpture absent. Columella with five strong plaits and three or four other weaker plaits inserted between the others. Siphonal notch and fasciole barely developed.

Colour pattern of numerous thin, anastomosing, axial, chestnut lines over the whole shell and on the body whorl, two dark reddish bands at the posterior and anterior third of the whorl.

Animal very similar to that of *N. amicula*. Foot broad, flat, entire; siphonal appendages short, paired and equal; tubular salivary gland of digestive system, short, paired and easily separated from the racemose salivary gland. Radula uniserial, tricuspid with the central cusp the larger.

Colour of animal white with a network of numerous thin chestnut lines.

DIMENSIONS:	Holotype C 108644 a	L 48	HA 41	W 20
	Paratype C 108644 b	L 39	—	W 17
	Paratype C 109012	L 40	HA 34	W 17

LOCATION OF TYPES: Australian Museum, Sydney: Holotype C 108644 a, Paratype C 108644 b, collected W.F. Ponder, I. Loch and P. Terrill, 14 Dec. 1977; Paratype C 109012 collected P. Colman and F. Rowe, 17 Nov. 1977.

TYPE LOCALITY: Capricorn Channel, 42 km N.E. of Lady Musgrave Is., Queensland, 23° 38.8'S, 152° 45.5'E, 365 m, 1977. *Kimbla* Cruise Station 24, 14 Dec. 1977.

OCCURRENCE: 40 km E. of Lady Musgrave Is., Queensland, 24° 44'S, 152° 49'E, 348-357 m shelly grey ooze, 1977, *Kimbla* Cruise Station 2, 17 Nov. 1977. 39 km E. of Lady Musgrave Is., Queensland, 23° 33.7'S, 152° 37'E, 348-339 m 1977 *Kimbla* Cruise Station 3, 17 Nov. 1977. East of North West Is., Capricorn Channel, Queensland, 23° 19.5'S, 152° 35.4'E. 320 m globigerine mud, 1977 *Kimbla* Cruise Station 23, 14 Dec. 1977.

MATERIAL: Types, two adults and four juvenile specimens and six fragments.

COMMENTS: This species most closely resembles the Middle Miocene *N. limbata* (Tate) from Victoria from which it differs by the dome-like, rather than pupiform protoconch, by the complete absence of spiral sculpture and the lack of lamella extension of the posterior part of the whorls, typical of the latter.

From *N. ralphi* (Finlay), it differs by its more slender and elongate shape and relatively low spire. The dark spiral bands of the colour pattern are somewhat similar to those preserved on *N. limbata*. Neither *N. ralphi* nor *N. limbata* have the subspinose nodules as sharply developed as in *N. inopinata*. Of the living species of the genus, *N. parabola* Garrard from southern Queensland and northern New South Wales has a similar colour pattern, but is half the size with a gradate spire

and prominent spinose shoulders. *N. capricornea* (Wilson) from Western Australia, has a more conical spire, is two-thirds the size, has no subspinose nodules and lacks any linear type colour pattern. This latter species also lacks spiral sculpture.

A specimen of *Nannamoria amicula* (Australian Museum C 94314), dissected by the author, has a morphology virtually identical to that of *N. inopinata*. The radula is also similar. *N. guntheri* (National Museum of Victoria F 27907) and, indeed, a large number of species of *Amoria*, which the author has examined, also have similar anatomical morphologies except that the radula is unicuspid.

ACKNOWLEDGEMENTS

I am grateful to Dr. W.F. Ponder, Australian Museum for making the material available and to his staff for sorting it out from voluminous dredgings. The photographs are the work of Mr. F. Coffa, National Museum of Victoria and I acknowledge with thanks the care he has bestowed upon them.

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ECOLOGICAL SEGREGATION AMONG NERITES AT NORTH-WEST CAPE, WESTERN AUSTRALIA

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SUMMARY

The ecological segregation of nerites was examined both horizontally and vertically. Two groups of species were found. *Nerita undata* and *N. chamaeleon* inhabit the rocky shores of the Exmouth Gulf side of North-West Cape where the water has a high silt content. *Nerita plicata* and *N. albicilla* live on the Indian Ocean side of the Cape where water turbidity is low. The temperate species *N. atramentosa* extends as far north as the southern end of North-West Cape, where it occurs sympatrically with *N. plicata* and *N. albicilla*. In each group of species one lives high on the shore (*N. undata* or *N. plicata*) and one is lower (*N. chamaeleon* or *N. albicilla*). Where *N. atramentosa* occurs it occupies an area slightly above *N. albicilla* and below *N. plicata*. These findings are compared with the results of other studies on the patterns of ecological segregation in nerites.

INTRODUCTION

Paine (1962) pointed out that to coexist successfully potential competitors must each utilize one or more aspects of the common environment more effectively than the competing species. If this was not done competitive pressures would lead to the exclusion or modification of the less well adapted species. The mechanisms by which closely related species living sympatrically utilize and partition the available resources have received an increasing amount of attention from marine biologists. Molluscs have been particularly useful in these investigations. The pioneering work of Kohn (1959) on the genus *Conus* on intertidal beachrock platforms in Hawaii is well known. The studies were later extended to other areas of the Indo-Pacific (Kohn, 1966; 1967; 1968). Paine (1962) investigated overlap in the genus *Busycon* in Florida and examined the trophic structure of molluscs in an area of Alligator Harbor, Florida, which had two pairs of congeneric species (Paine, 1963).

In the years since Paine's 1963 paper a number of studies of this type have been conducted on a variety of molluscan groups, including nerites. Nerites are particularly useful for a number of reasons. The family Neritidae has over 200 species worldwide (Russell, 1941). The genus *Nerita* is widely distributed on rocky shores, and there are often several species inhabiting a particular area. The species are moderately large, have high population densities and are well known taxonomically. All are herbivorous; they

feed by rasping algae from the rocks on which they live. The ecology and physiological ecology of nerites have been investigated in several areas: the Caribbean Sea (Kolipinski, 1964; Chisslett, 1969; Lewis et. al., 1969; Lewis, 1971), the Red Sea (Safriel, 1969), the Indian Ocean (Hughes, 1971), and Australia (Underwood, 1975; 1976; Coleman, 1976; Wells, 1978).

Shallow-water molluscs exhibit three distributional patterns in Western Australia (Wilson and Gillett, 1971; Wells, 1979). There is a warm temperate fauna on the south coast which extends northwards along the west coast of the state. A tropical fauna on the north coast extends southward along the west coast. The warm temperate and tropical faunas overlap extensively on the west coast. In addition 8 to 9% of the shallow-water molluscs are endemic to Western Australia. Eight species of *Nerita* occur in the state: 7 are tropical, one is temperate, and none is endemic. The area of greatest species overlap of this genus is at North-West Cape, at the extreme northern end of the west coast overlap zone. Five nerites, four tropical and one temperate, are found at North-West Cape (Wells, 1979). It is this area that will be investigated in the present paper.

MATERIALS AND METHODS

Nerites were examined at 10 stations on North-West Cape (Figure 1.) in July and August 1977. Detailed studies were made at Coral Bay (Station 1), Yardie Creek (4), 10 km south of Yardie Creek (3), and Bundegi Reef (8). At each of these stations the intertidal limestone reef had a vertical face which extended from the supratidal area into the lower intertidal region. A gently sloping beachrock platform led from the base of the vertical face into the subtidal zone. Five transects 10 m apart were made at each station. A rope was run from the high tide line down the shore at the bottom of the nerite zone. Beginning at the high tide line a quadrat 3.0 m long and 0.5 m wide was delineated by ropes. All nerites in each quadrat were collected, identified, and measured with calipers. Vertical height on the shore was determined by comparing the level reached at high tide with the tidal prediction for Pt. Murat on the tip of North-West Cape (Australian Hydrographic Service, 1977). The mean difference between successive high and low tides is 1.0 m; the maximum during 1977 was 1.7 m.

Supplementary examinations were made at the six remaining stations (Numbers 2, 5, 6, 7, 9, and 10 on Figure 1). At these stations the beachrock was searched qualitatively to verify the patterns recorded at the four detailed stations. The nerite species present and their positions on the shore were determined.

The overlap of nerite populations on the shore was determined using the index of species overlap developed by Horn (1966). This index is modified from earlier versions proposed by Simpson (1949) and Morisita (1959). The index varies from 1 to 0. A value of 1 signifies complete overlap of populations and 0 indicates complete separation.

RESULTS

Yardie Creek (Station 4)

Three species of nerites, *Nerita undata*, *N. albicilla*, and *N. plicata* were collected at this station. Both *N. undata* and *N. albicilla* were too rare to be examined quantitatively. *Nerita plicata* was common on the upper shore levels. The mean shell length of this species was 23.7 ± 5.2 mm. Its mean shore height was 2.2 ± 0.4 m. The few *N. albicilla* that were collected averaged 1.8 m on the shoreline, 0.4 m below the average of *N. plicata*.

10 km south of Yardie Creek (Station 3)

Four species were found at this station: *Nerita plicata*, *N. albicilla*, *N. atramentosa*, and *N. undata*. *Nerita atramentosa* and *N. undata* were too rare to be examined quantitatively. The mean shell lengths of the most common species were almost identical: 20.3 ± 6.5 mm for *N. plicata* and 21.0 ± 2.6 mm for *N. albicilla* (Table 1 and Figure 2). The difference was not statistically

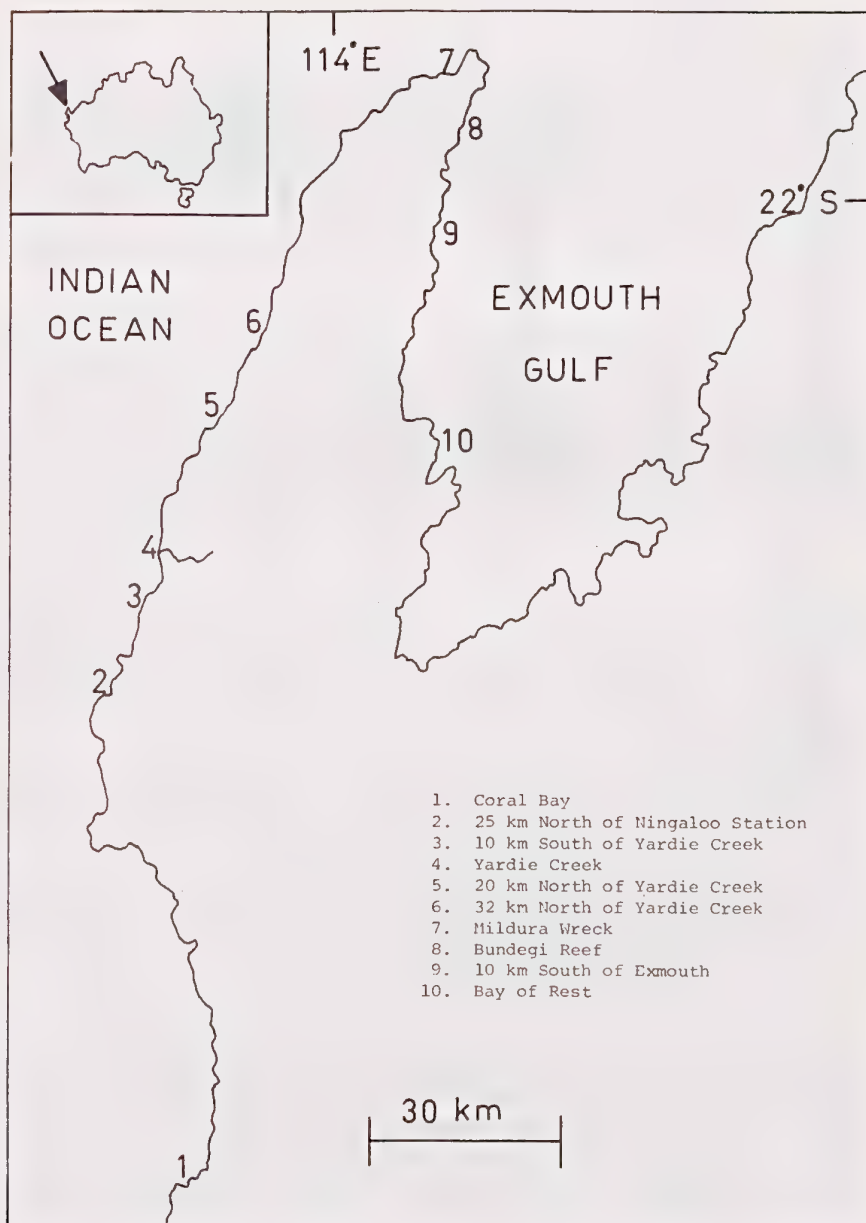


FIGURE 1. Map of North-West Cape, Western Australia, showing the locations of the sample sites.

significant (t-test, 0.05 level). The mean shore heights differed substantially between the two species (Figure 3). *Nerita plicata* averaged 2.6 ± 0.1 m; *N. atramentosa* was 2.0 ± 0.1 m. The vertical overlap on the shore was calculated to be only 0.01.

Coral Bay (Station 1)

Three nerites were found at Coral Bay: *Nerita plicata*, *N. albicilla* and *N. atramentosa*. *Nerita plicata* was distributed along the upper intertidal above the level of *N. atramentosa*, but it was rare and did not appear in the quantitative transects. The mean length of *N. albicilla* at Coral Bay was 20.6 ± 1.5 mm. *Nerita atramentosa* averaged 17.9 ± 3.3 mm (Table 1 and Figure 2). The difference was not statistically significant (t-test, 0.05 level). *Nerita albicilla* and *N. atramentosa* occupied overlapping areas on the shoreline (Figure 3). *Nerita atramentosa* was a little higher up, with a mean of 1.9 ± 0.6 m; *N. albicilla* averaged 1.8 ± 0.5 m. The difference on the shore, while consistent, was not statistically significant (t-test, 0.05 level). The index of overlap calculated for the two species was 0.38.

Bundegi Reef (Station 8)

Two species were present at Bundegi Reef: *Nerita undata* and *N. chamaeleon*. *Nerita undata* averaged 16.5 ± 5.8 mm in shell length and *N. chamaeleon* 13.7 ± 3.9 mm (Figure 4). The difference was not statistically significant (t-test, 0.05 level). *Nerita undata* inhabited the upper intertidal zone and had a mean shore height of 2.1 ± 0.2 m. *Nerita chamaeleon* was lower, with a mean of 1.7 ± 0.4 m (Figure 4). The difference in shore height was statistically significant (t-test, 0.05 level). *Nerita chamaeleon* occupied the lower part of the vertical cliff face, and extended onto the gently sloping beachrock platform below the cliff. The index of overlap between the two species was 0.14.

Other stations

The same patterns of nerite distribution were found at the six qualitative stations. At all stations on the west side of North-West Cape (Figure 1, Stations 2, 5 and 6) *Nerita plicata* and *N. albicilla* were the dominant species. *Nerita plicata* always occurred in the upper intertidal zone and *N. albicilla* was below it. Small numbers of *N. atramentosa* were found at Station 2, 25 km north of Ningaloo Station. *Nerita undata* on the upper shore and *N. chamaeleon* on the lower shore were the only two nerites collected at Stations 9 and 10 on the Exmouth Gulf side of North-West Cape.

Thus the stations on the western side of North-West Cape were dominated by *N. plicata* and *N. albicilla*; those on the eastern side were dominated by *N. undata* and *N. chamaeleon*. The key question is whether there is a rapid transition between the two dominant groups at the tip of North-West Cape, or if the transition is gradual. The rocky shore nearest the tip of the Cape was at Station 7, between the northern extremity of North-West Cape and Vlaming Head. Nerites at this station were too scattered to sample quantitatively. A thorough search of the beachrock revealed only *N. plicata* and *N. albicilla*. The nearest rocky shore on the east side of North-West Cape is at Bundegi Reef (Station 8), where *N. undata* and *N. chamaeleon* dominated. Thus the species present on the shoreline switched completely between Stations 7 and 8.

DISCUSSION

The five species of nerites at North-West Cape have been shown to be separable into two groups. The beachrock on the Indian Ocean (west) side of the Cape supports populations of two tropical species: *Nerita plicata* in the upper intertidal and *N. albicilla* lower down. *Nerita atramentosa* occurs at the southern end of North-West Cape where it occupies a shore position intermediate between *N. plicata* and *N. albicilla*. Two other nerites, *N. undata* and *N. chamaeleon*, occur on the Exmouth Gulf (east) side of North-West Cape. *Nerita undata* lives higher on the shore than *N. chamaeleon*. The factors causing the separation of the nerites into distinct groups on the two sides of North-West Cape are unknown, but the situation parallels the distribution of echinoderms in Queensland reported by Eudean (1957). The echinoderms were divided into an inshore fauna that lives in areas of high turbidity and low salinity and an offshore group of species that inhabit coral areas of high salinity and low turbidity. Exmouth Gulf has a high turbidity, and much of the shoreline is fringed with mangroves. *Nerita lineata* Gmelin, 1791 is the only nerite occurring in the mangrove

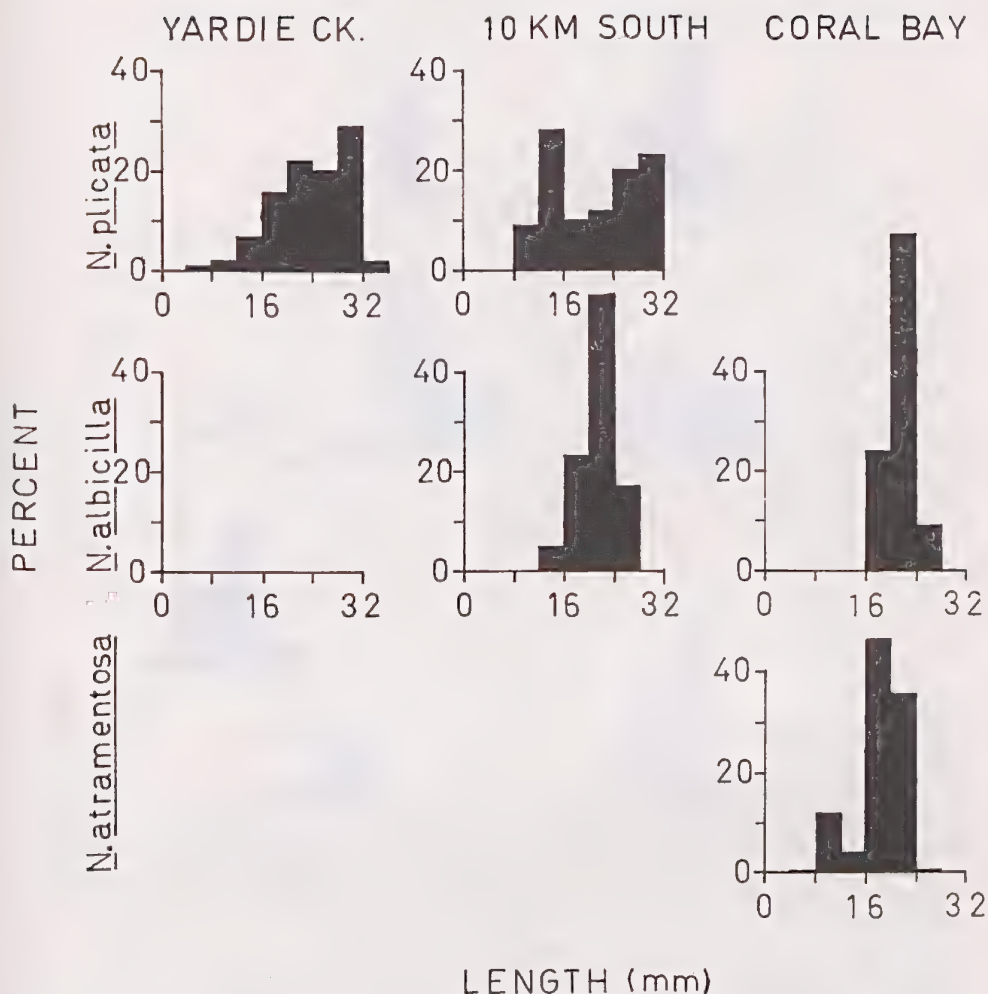


FIGURE 2. Size-frequency graphs of *Nerita* collected at three quantitative stations on the west coast of North-West Cape.

swamps. The waters of the west side of North-West Cape have a low turbidity and the shoreline is fringed with coral reefs.

Differential zonation of nerites on a shoreline is well known (Kolipinski, 1964; Hughes, 1971; Wells, 1978). The study most comparable to the present investigation was conducted in the Admiralty Gulf, Western Australia (Wells, 1978), using the same methods used at North-West Cape. Three nerites were studied on a rocky shore in the Admiralty Gulf. The shore was composed of loose rocks ranging from a few centimeters to 0.3 m in diameter. *Nerita reticulata* Karsten, 1789 had a mean shore height of 3.0 ± 2.5 m; *N. undata* was 3.9 ± 2.6 ; and *N. polita* Linnaeus, 1758 was 5.2 ± 0.2 m. The index of overlap between adjacent species pairs was 0.29 for *N. undata* - *N. polita* and 0.35 for *N. reticulata* - *N. undata*. Both figures are higher than those of 0.01 recorded 10 km south of Yardie Creek and 0.14 recorded at Bundegi Reef on North-West Cape. The highest overlap found at North-West Cape was for *N. albicilla* - *N. atramentosa*, which had an overlap of 0.38. These species do not occur together over most of their ranges. Thus in both areas of Western Australia that have been studied the nerites show a clear segregation by shore height.

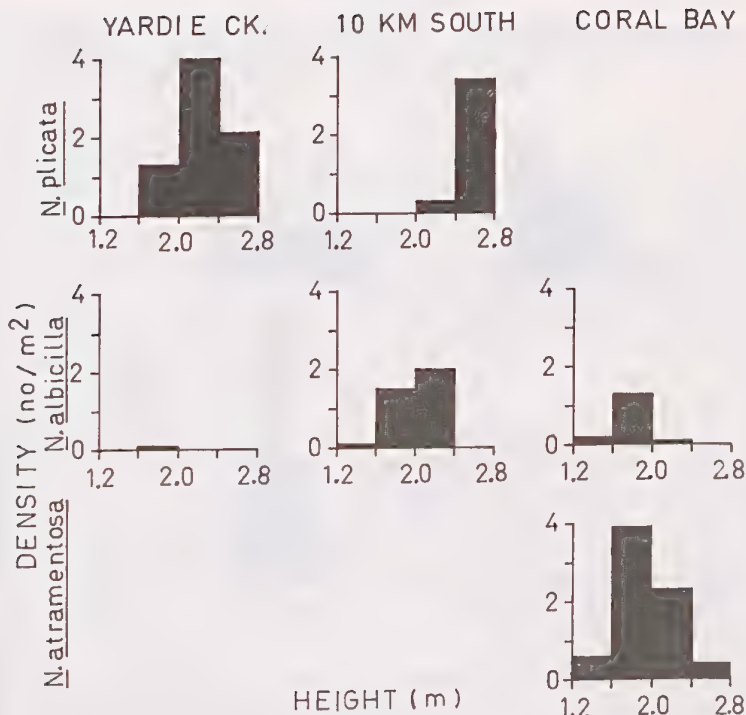


FIGURE 3. Tidal heights of *Nerita* collected at three quantitative stations on the west coast of North-West Cape.

There is some indication that the vertical distribution of *Nerita plicata* on the shore was affected by *N. albicilla*. At Yardie Creek (Station 4), where *N. albicilla* was rare, *N. plicata* was widely distributed between 1.6 and 2.8 m on the shoreline, and had a mean shore height of 2.2 ± 0.4 m. *Nerita albicilla* was common at the station 10 km south of Yardie Creek (Station 3), where it had a mean shore height of 2.0 ± 0.1 m. *Nerita plicata* at this station were higher on the shore than at Yardie Creek. Only a few individuals were found below 2.4 m, and the mean shore height of the species was 2.6 ± 0.1 m, 0.4 m higher than at Yardie Creek.

Congeneric species living at different shore levels where immersion and emersion times are different presumably have different specializations developed to withstand the microenvironments. Little work has been done on this aspect of the biology of nerites. Coleman (1976) investigated the ability of three species (*Nerita albicilla*, *N. plicata* and *N. polita*) to respire aerially. All three species consumed oxygen at similar rates, indicating that the ability to respire aerially during emersion is not an important factor in determining the vertical distribution of nerite species.

The three species studied in the Admiralty Gulf showed a clear segregation by size: *N. reticulata* averaged 9.4 ± 0.7 mm; *N. undata* 13.0 ± 2.1 mm; and *N. polita* 16.1 ± 1.6 mm (Wells, 1978). The possibility of character displacement similar to that found in mud snails of the genus *Hydrobia* by Fenchel (1975) was suggested. This does not appear to occur at North-West Cape, except possibly at Bundege Reef, where *N. undata* averaged 16.5 ± 5.8 mm and *N. chamaeleon* were 13.7 ± 3.9 mm.

Densities in the Admiralty Gulf were much higher than at North-West Cape. The maximum density attained by *Nerita undata* at Bundege Reef was $9.0/\text{m}^2$. In the Admiralty Gulf it reached $20.3/\text{m}^2$ and *N. reticulata* had a maximum of $35.9/\text{m}^2$ (Wells, 1978). The other species at North-West Cape did not have densities greater than $4.0/\text{m}^2$. The shorelines of the two areas were different and no doubt affected the *Nerita* populations. The beachrock platforms at North-West Cape are solid cliffs with few nooks and crannies to provide protection for snails. The rocky shore in the Admiralty Gulf had small rocks piled several deep, providing substantial protection. The

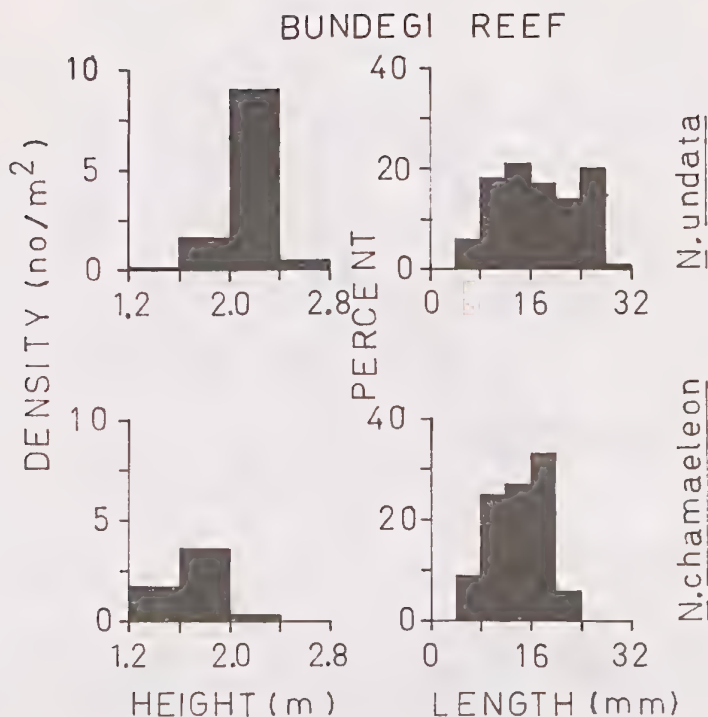


FIGURE 4. Tidal height (left) and size-frequency graphs (right) of *Nerita* collected at Bundegi Reef on the east coast of North-West Cape.

differences in density observed in the two areas could also be a result of differing amounts of food resources along the shorelines. Competition for food among congeneric species of carnivorous gastropods is well known (Kohn, 1959; 1966; 1967; 1968; Paine 1962; 1963), but herbivorous species have not been investigated in detail. Underwood (1976) has demonstrated that food competition does occur within populations of *Nerita atramentosa*, and it is quite possible that it also occurs between species.

ACKNOWLEDGEMENTS

I thank A. Brearley and P.M. Summerfield for assistance in the field. Dr D. Roberts of Queen's University of Belfast, Northern Ireland criticized the manuscript.

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Table 1. Population characteristics of nerites collected at North-West Cape.

	Yardie Creek		10 km south		Coral Bay		Bundegi Reef	
	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)
<i>Nerita plicata</i> Linnaeus, 1758	23.7 ± 5.2	2.2 ± 0.4	20.3 ± 6.5	2.6 ± 0.1	--	--	--	--
<i>Nerita albicilla</i> Linnaeus, 1758	Present	1.8	21.0 ± 2.6	2.0 ± 0.1	20.6 ± 1.5	1.8 ± 1.5	--	--
<i>Nerita atramentosa</i> Reeve, 1855	--	--	Present	Present	17.9 ± 3.3	1.9 ± 0.6	--	--
<i>Nerita undata</i> Linnaeus, 1758	Present	Present	Present	Present	--	--	16.5 ± 5.8	2.1 ± 0.2
<i>Nerita chamaeleon</i> Linnaeus, 1758	--	--	--	--	--	--	13.7 ± 3.9	1.7 ± 0.4

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REDESCRIPTION OF *HELICARION CUVIERI* FROM SOUTHERN
TASMANIA AND *HELICARION FREYCINETI* FROM NEW SOUTH WALES
(PULMONATA: HELICARIONIDAE).

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SUMMARY

The shell and anatomy of *Helicarion cuvieri* Ferussac 1821 are redescribed and a neotype designated. The lectotype designated for *Helicarion freycineti* Ferussac 1821 is described with notes on the external features of the animal.

INTRODUCTION

Before the species *Helicarion rubicundus* Dartnall & Kershaw 1978 could be described, the type species of *Helicarion* required clarification. The type, *H. cuvieri* Ferussac, established by subsequent designation by Gray (1847) and the genus require more detailed description for stability. The type specimen of *H. cuvieri* was described as a shell with retracted animal in preservative apparently in the Paris Museum. Enquiries reveal that it is not in Paris, nor could it be located elsewhere. As French expeditions have collected in southern Tasmania this would be the most probably type locality. The taxonomic importance of the species to the family Helicarionidae requires the erection and description of a neotype. Enquiries concerning *H. freycineti* made at the same time established that syntypes existed in the Paris Museum. One of these shells is here selected as lectotype and is described.

HELICARION CUVIERI FERUSSAC

The significance of the type species of *Helicarion* to the Helicarionidae, very much as Australian sub-family (or family), requires species stability. Other Australian genera and new species held by authors outside Tasmania cannot be clearly established. Hedley (1891) and Semper (1885) described and figured the anatomy but neither define an adequate locality. Semper states "Van Diemensland. Zwei Exemplare durch V. Martens." Most authors, occupied with other groups, make only passing reference to the species (e.g. Rensch, 1932). Semper's figure 7 (i.e., plate 3) is sufficient for broad comparative use. Although Gray (1847, p. 169) designated *H. cuvieri*, some authors (e.g. Fischer, 1887) continued to use *H. freycineti*. This species also needs clarification. The next earliest species, *H. niger* (Quoy & Gaimard, 1832), has an existing type which will be described in a future paper.

Enquiry for the type of *H. cuvieri* has been fruitless. M. Tillier of the Paris Natural History Museum wrote that "the original material of *H. cuvieri* Fer"....."were already missing...Chevallier made his

review of the Ferussac collection (Bull. Mus. Hist. Nat., Paris, 37, no. 1, 1965, p. 167)". M. Tillier thought it possible that the specimen could be in the Deshayes collection, partly in the Ecole des Mines, but his enquiries there and elsewhere gave no result. Dr. Mordan sent a list of British Museum *Helicarion* material and European museums have assisted. Dr. B.J. Smith, while in Europe, looked further at the available material and following further discussion concluded the type was lost.

The precise type locality for *H. cuvieri* is unknown. Mt. Wellington is an obvious possibility but very little material is known from the region. A suitable population with long term stability was found near the Strathgordon Road, south from Maydena in south-west Tasmania. This site, which provides for adequate study, has been chosen as the 'type locality' for the neotype. Comparison indicates this population to be consistent with other southern material. The neotype has been lodged in the Paris Museum and voucher specimens placed in eastern Australian museums.

Among the synonyms listed *Helicarion verreauxi* has been recorded from Tasmania. Mt. Wellington is mentioned and Verreaux may have collected there but no material has been found specifying a locality. Possible type material of this 'species' is in the British Museum (N.H.) with the registered number 197780. It is labelled "Australia" with a pencilled note "Type on the right". At best it is a synonym but the evidence does not give the specimens syntype status. Two other names must be considered. Legrand in the first edition of his Monograph introduced *Helix vitrinaformis* which Cox, not having seen the animal, described for him as a new species. Petterd replaced this preoccupied name with *Helix buttoni*. Petterd & Hedley (1909), believing it to be *H. cuvieri*, discarded the name. Their comment that the name cannot be authenticated with a known shell can be considered accurate. The description of *Helicarion cuvieri* which follows is based on animals from both the neotype locality and from other areas.

DESCRIPTIONS

HELICARION CUVIERI FERUSSAC 1821

FIGURES 1-15

- 1819. *Helicarion cuvieri* Ferussac, *Hist. Moll.*, pl. 9, f. 8; 4 July.
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- 1825. *Vitrina cuvieri*. Gray, *Ann. Phil.*, 9 : 408.
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- 1871. *Helix vitrinaformis* Legrand, *Coll. Mon. Tasm. Land. Shells*, sp. 58
- 1871. *Vitrina (Helicarion) verreauxi*. Legrand, *op. cit.*, ed. 2, sp. 2.
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DIAGNOSIS: *Helicarionid* snail with shell small to medium size, depressed sub-globose pale yellow, light orange yellow to light orange glassy sometimes tinted green; spire flatly convex, sutures shallow very narrowly margined, imperforate, aperture oval curving gently from body; animal various shades of grey often tinted pink or mauve, sometimes cream. Radular rachidian elongate narrow distinctly excavate, penial verge or pilaster absent.

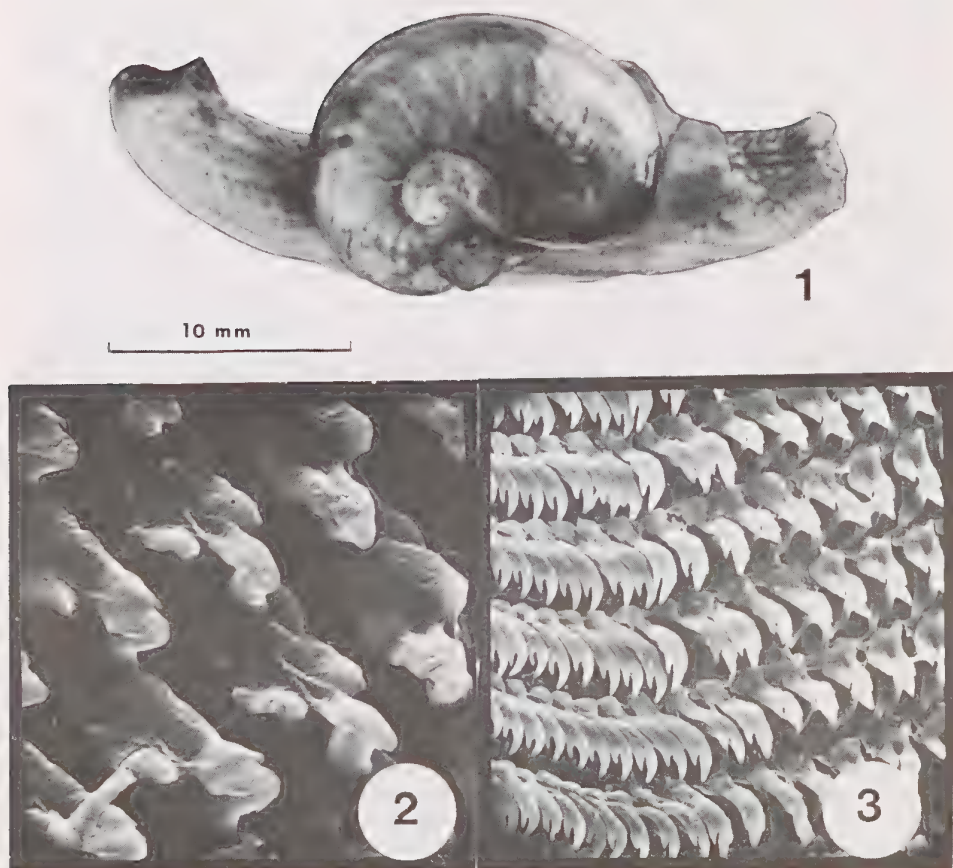
Shell (fig. 15) 3.25 whorls rarely larger, revealing body colours usually shades of yellow or orange in cream animals. Protoconch about 1.75 whorls pale, off-white or tawny grey ending at fine curved varix or depression; sculpture fine irregular variable microscopic rounded radial lirae cut by faint spiral striae sometimes minutely beaded, interstices minutely pustulate; juvenile brief, fine close

radial lirae. Whorl rapidly expands to adult of variable wave-like riblets, minute radial lirae may superimpose, riblets may be sharpened, usually strengthen near sutures on body whorl, surface can be weakly undulate, spiral striae very close very weak. Suture margin never significant; aperture lunate oval regularly gently curving from body, upper lip can straighten with maturity, columella weak membranous.

Animal grey with pinkish or mauve tints, darker dorsally, sometimes creamy, off-white or very dark grey, body tubercles may be grey with pinkish interstices, caudal margin can be off-white. Ocular tentacles (OT) dark grey or black, inferior greyish (fig. 9). Lappetts usually paler than body, fringed grey, right pallial lappett (RPL) with two small warts (fig. 12) dark or pale, mid-basal and posterior. Foot sole pale tripartite, central section broadest centrally, one-quarter to one-third of width tapering gradually but rapid over one-third of posterior length, almost flat; sole vertical margins slightly convex with a narrow line of tubercles above peripodial groove. Foot distinctly recessed about 1 mm beneath muzzle. In a shell of dimensions 12 mm max., 10.7 mm min. diameter the elongate right pallial lappett extends 6.7 mm from suture at aperture, 4 mm widest with basal wart 3 mm from extremity, left pallial lappett (LPL) 5.5 mm long 3.5 mm max. width, elongate triangular with two small warts, (fig. 12) extends around upper lip; right body lappett (RBL) an extension of pallial lappett, 4 mm long, 1 mm below pneumostome; mantle (M) distinct from lappett, variable, one specimen had mantle extending 2 mm from shell, 4 mm from ocular tentacles; muzzle extends 2 mm from ocular tentacles which are 1.5 mm apart, ornamented with small rounded tubercles, inferior tentacles smooth. Genital atrium (GA, fig. 5) below slightly posterior to right ocular tentacle, distinct oval or slit-like, lip smooth, adjacent tubercles slightly raised, penis white. Pneumostome slit-like or oval 0.8 mm wide defined with white tissue, may bulge. Foot bulging centrally, tail flattened below visceral mass, posterior keel one-quarter to a little more than one-third of tail length passing on to produced caudal horn. Body (fig. 1) ornamented with variable diamond shaped tubercles less defined below viscera, parallel on anterior dorsum, sloping posteriorly from posterior dorsum; an oblique line of tubercles always present sloping to atrium.

ANATOMY

Buccal mass (BM, fig. 9) elongate sub-rounded, jaw (fig. 10) arcuate translucent orange yellow or yellow with pale orange pointed extremities, cross section triangular, 1.5 mm wide, 0.4 mm thick, central protuberance rounded passing into small transverse ridge. Radular (figs. 2, 3) formula 30.14.1.14.30 of about 130 rows. Rachidian tricuspid with very narrow elongate mesocone curving from narrowly rounded tip, through a distinctly elongate excavation to a raised point between ectocones; ectoconal cusps set slightly more than one-half distance posteriorly, rather broad strong curved above, moderately pointed sloping posteriorly. Rear of tooth distinctly narrowed clearly curved. Lateral teeth with sub-elongate robust mesocone, a very small endoconal cusp protrudes a little less than one-fifth the distance from mesocone tip, ectoconal cusp in line with rachidian ectocone, curved bulging slanting to a point about one-half tooth length with clear excavation between ectocone and opposing lateral ridge of mesocone, a distinct sub-triangular minute cusp protrudes centrally between tip of ectocone and tip of mesocone, tooth posterior broad curved. Marginal teeth strongly curved with ectocone clearly posterior to mesocone slightly inwardly hooked, both cusps narrowly pointed. Rachidian base plate broad laterally convex strongly curved about posterior of next tooth with strong upright column to mesocone almost at tip. Lateral base plates elongate passing clearly below posterior of next tooth, column upright then slanting forward to mesocone cusp, base curved toward then away from rachidian base. Dartnall & Kershaw (1978, p.5) give a comparison of southern species. Reproductive system (figures 4-8): Penial complex commonly doubled into a partial figure of eight with retractor muscle (RM) at extremity of curve. Penis (P) expands distinctly then contracts variably to junction with epiphallus (EP); penial sheath (PS) very thin white transparent attached near atrium (GA), sheath retractor (PR) very thin elongate passing to penial retractor through connective tissue between arms of epiphallus. Penial retractor (RM) arises from very small straight transparent base which is traversed by a white vein (PV) passing through viscera adjacent to stomach (S) near pericardium (PC) to pallial system. Caecum absent. Flagellum (Q) distinctly sinuate (figs. 5, 8), normally less than one-fifth complex length, consisting largely of a defined lumen which I called the epiphallic gland (Dartnall & Kershaw, 1978, p. 3) externally ornamented with protuberances about curve of sinuation and two distinct lateral bulges.



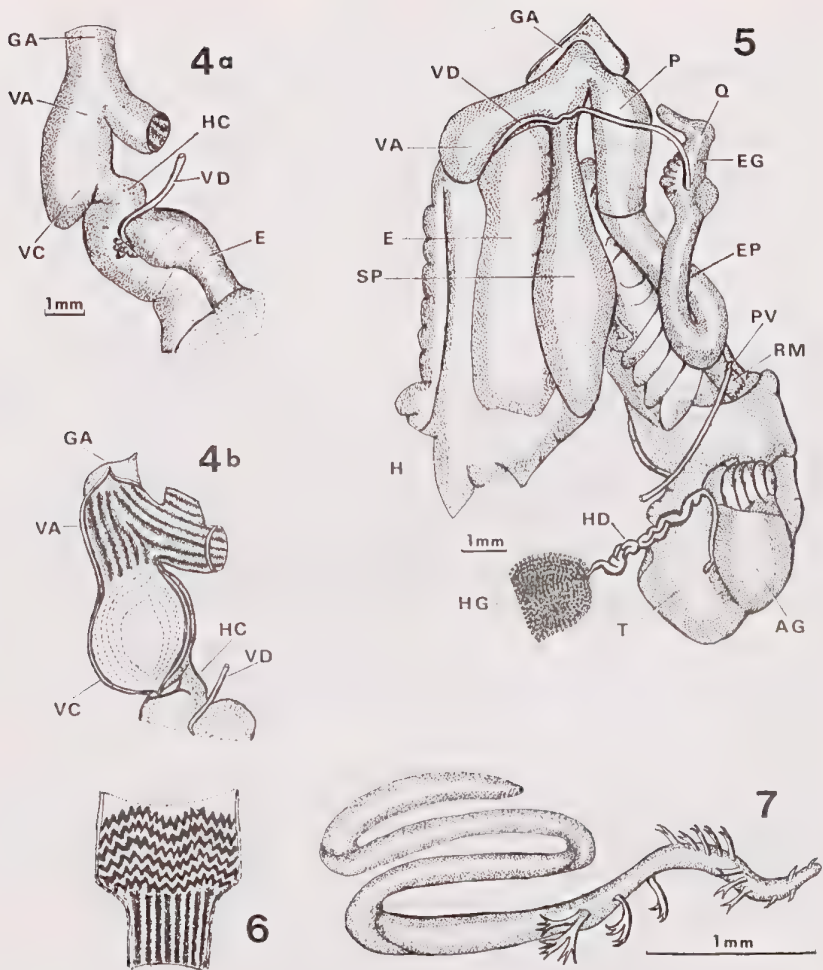
FIGURES 1-3

1. *Helicarion cuvieri* Ferussac .Neotype.

2. Radula: central and lateral teeth x 1400. SEM by Dr. B.J. Smith.

3. Radula: lateral and marginal teeth x 500. SEM by Dr. B.J. Smith.

Vas deferens (VD) inserts 1 mm - 1.5 mm from flagellum extremity adjacent and slightly lateral to bulge at a point three to four-fifths length of flagellum, transversely central but slightly variably situated. Epiphallic duct (EP) lined throughout with longitudinal pilasters minutely folded near flagellum, ending abruptly at penial junction (fig. 6) usually at a relatively slight constriction. Penis (fig. 6) lined with transverse folded lamellate pilasters. Verge or vergic pilaster absent, dart sac or sarcobellum absent. Spermatophore (fig. 7) with 15, mostly branching, spines somewhat variably spaced generally evenly distributed, the two largest corresponding with flagellum lateral bulges, the remainder with lateral sinuate curve. Internally these ornaments are crypt-like and form the spermatophore mould; when empty they are visibly interconnected. Bursa copulatrix (SP) very elongate pyriform with duct, opening from the small atrium (fig. 8), a narrow muscular peduncle one-third length of combined bursa and peduncle, lined with low rounded pilasters (fig. 4b) curving from atrium where broadly thickened. Bursa internally capacious, transversely lined with very thin transverse plicae some converging, variable bulging with contents. One specimen contained two complete spermatophores, another an encapsulated partly digested spermatophore. Subsharpened pilasters pass from atrium to vagina (VA, fig. 4b) adjacent to pilasters curving from bursa duct to entrance to an enlarged vaginal chamber (VC) (possibly a primitive homologue to the atrial



FIGURES 4-7

- 4a. Vagina-spermoviducal junction enlarged.
 4b. Section through vagina, bursa duct, atrial junction enlarged.
 5. Reproductive system.
 6. Section through junction of penis and epiphallus.
 7. Spermatophore of *H. euvieri* Fer.

AE - anterior oesophagus, AG - albumen gland, BG - buccal ganglia, BM - buccal mass, C - crop, CG - cerebral ganglia, DG - digestive gland, E - prostate, EP - epiphallus, EG - epiphallic gland, GA - genital atrium, H - uterine complex, HC - uterine duct, HD - hermaphrodite duct, HG - hermaphrodite gland, KD - kidney, LPL - left pallial lappett, OR - ocular retractor, M - mantle, P - penis, PaG - parietal ganglia, PC - pericardium, PE - posterior oesophagus, PeG - pedal ganglia, PG - pleural ganglia, PR - penial sheath retractor, PS - penial sheath, PV - penial retractor vein, Q - flagellum, R - rectum, RM - penial retractor, RBL - right body lappett, RPL - right pallial lappett, S - stomach, SP - bursa copulatrix, T - talon, U - ureter, VA - vagina, VC - vaginal chamber, VD - vas deferens.

diverticulum of Van Mol, 1970) from which a very short uterine duct (HC) passes to the spermo-viducal complex (figs. 4a, 4b). The strongly curved vas deferens inserts terminally with prostate (E) an off-white to cream minutely tubular organ of variable width adherent to the pale grey uterine section (H), the whole arising from the sub-cubic off-white, pale grey or pale buff albumen gland (AG, fig. 5). Hermaphrodite gland (HG) a sub-globular mass of very small acini embedded near apex of digestive gland (DG) visible as section across upper whorl; hermaphrodite duct (HD) yellow contorted short inserting with albumen gland within a shallow recess (fig. 5) on anterior aspect near junction with spermo-viducal complex, becoming a fine duct immersed below surface along alignment of recess to the 0.3 mm long very thin digitiform talon (T) embedded 2 mm below surface where duct branches to carrefour; talon white with some black capillaries on duct and talon surfaces. Talon structure in *Helicarion* described by Van Mol (1973). The albumen gland is situated between the anterior oesophagus, stomach and pallial wall, hence is visible through the shell; the bursa copulatrix is situated latero-dorsally and the penial complex dorsally to the spermo-viducal complex (fig. 5). The right ocular tentacle passes dorsally over the penis to the retractor below the spermo-viducal complex (fig. 9). Digestive complex (fig. 12): Buccal mass (BM, fig. 9) sub-rounded elongate 3.0 to 3.5 mm long, 2.5 mm diameter, retractors postero-laterally sub-terminal, anterior oesophagus (AE) with elongate rarely grossly expanded crop (C) commonly encased through much of its length in a sleeve of muscular and fatty tissue, expand into stomach (S); posterior oesophagus (PE) curves through the digestive gland recurving below stomach (not in a double coil as in *H. rubicundus*) about 20 mm long to rectal duct (R) opening to exterior dorsally just within pneumostome. Bilobate digestive gland (DG) pinkish to pale buff, kidney (KD) dorsal below pallial surface, cream elongate with primary ureter sharply recurving to secondary ureter (U) alongside rectum. Vascular, neural and muscular complex: Pallial surface vascularised, pericardium (PC) closely antero-laterally to kidney, auricle large with thin transverse lamellae internally (fig. 14), a thin central diaphragm has a small hiatus, main pallial vein clear, ventricle very small. Penial vein (PV) from pallial surface to penial retractor may provide pressure to penis. Circumoesophageal central nervous system situated posterior to buccal mass, the relationship depending on degree of retraction. Cerebral ganglia (CG, fig. 11) elongate ovoid slanting anteriorly and laterally to buccal mass joined by a short commissure, give rise to the nerves to the ocular tentacles (OT) and retractors (OR), inferior tentacles, buccal mass and ventrally to the penis from the right ganglion. Flexible cerobro-buccal commissures arise latero-ventrally passing to buccal ganglia (BG) which provide nerves to the oesophagus and pharynx, these and remaining ganglia encased in tissue. Pleural ganglia (PG) posterior to and slightly below buccal ganglia, with parietal ganglia smaller and ventral but dorsal to the pedal ganglia, with small visceral ganglion between. A count of eighteen connectors radiate fan-like to the body cavity from the pedal ganglia (PeG) which also provide nerves to the vagina, bursa, spermo-viducal complex, penis and vas deferens. A major nerve emerges between the right buccal and pleural ganglia laterally to penial retractor, another from the pleural ganglia to albumen gland; nerves from the parietal ganglia (PaG) connect posteriorly to the spermo-viducal complex. Minor nerves immersed in tissue connect pedal ganglia nerves to vagina anteriorly. The parietal ganglia provide nerves to the cavity floor and retractors but not all of these and others have been traced. Tentacular retractor muscles interconnect to pass down the right side of the oesophagus to the columella with the buccal retractors, the latter arising 2 mm from the muzzle pass below the cerebral ganglia. Strong muscles support the buccal - ganglionic system. Paired retractors pass to the posterior of the body cavity, another pair from the columella to body cavity walls laterally below ocular tentacles. Penial retractor connects with pallial floor. Penis, atrium and buccal muzzle all capable of eversion which is common when an animal is relaxed before fixing, suggesting that muscular relaxation has occurred. Comparison with other described species in Tasmania and Victoria is given by Dartnall & Kershaw (1978) for various features.

TYPE MATERIAL

Neotype (fig. 1): Museum National D'Histoire Naturelle, Paris; from litter in rain forest near Needles Picnic Ground south of Strathgordon road, south-west Tasmania. Grid reference topographical survey 1 : 100 000 sheet 8112 Wedge, 452500 ME 5265500MN, collected R.C. Kershaw 8 April, 1977; entire animal preserved in alcohol. Voucher material: two specimens Tasmanian Museum E10388, two specimens National Museum of Victoria No. F 30142, one specimen Australian Museum No.C.111938, one specimen Queen Victoria Museum 1978/9/1 QVM No. 355.

DIMENSIONS

		Length (mm)		Height	Approx. foot length (preserved)
		Maximum	Minimum		
Neotype		10.6	9.0	5.5	23
Vouchers					
E10388	a	11.0	9.0	5.8	24
	b	10.6	8.8	5.7	18
F30142	a	11.4	9.0	6.0	24
	b	10.0	8.6	5.2	20
C.111938		10.9	8.9	5.1	20
1978/9/1		8.7	6.9	5.0	18

DESCRIPTION BY FERUSSAC

"A very distinct species especially by its colouring. It is oval, sub-globular. Its spire very short, number of whorls four, barely convex and its increase in size is very rapid, the suture is simple and superficial. The last whorl is very large, wide on the top, convex at the circumference, a little depressed in the centre, ended by an aperture of medium size, oval, semi-lunar, almost as high as wide. The columella is short regularly curved, it is thin and sharp and continues without interruption with the right margin. The latter is barely convex in front, it is thin sharp and its membranous margin is bent back within as a result of the dessication of the shell. The whole surface is brilliant and polished and yet you notice on it a rather regular series of ridges in the form of little folds which are gradually reduced toward the aperture. Although thin and transparent this shell is of a brownish green darker than the majority of other species. It belongs to the genus *Helicarion* of Ferussac. Its animal contracted in the preservative has the foot strongly truncated behind by a large mucus crypt of which the opening resembles a small vault with a pointed arch. The shell is 14 mm long and 9 mm thick."

The neotype matches the original description in most aspects. A shell of four whorls is unlikely to be found, the largest seen being 3.6 whorls. A Maydena specimen in hand measures 13 mm by 9 mm. Few reach this size but shells of unknown locality have been seen. The colour is related to the environment.

ANATOMY ACCORDING TO HEDLEY

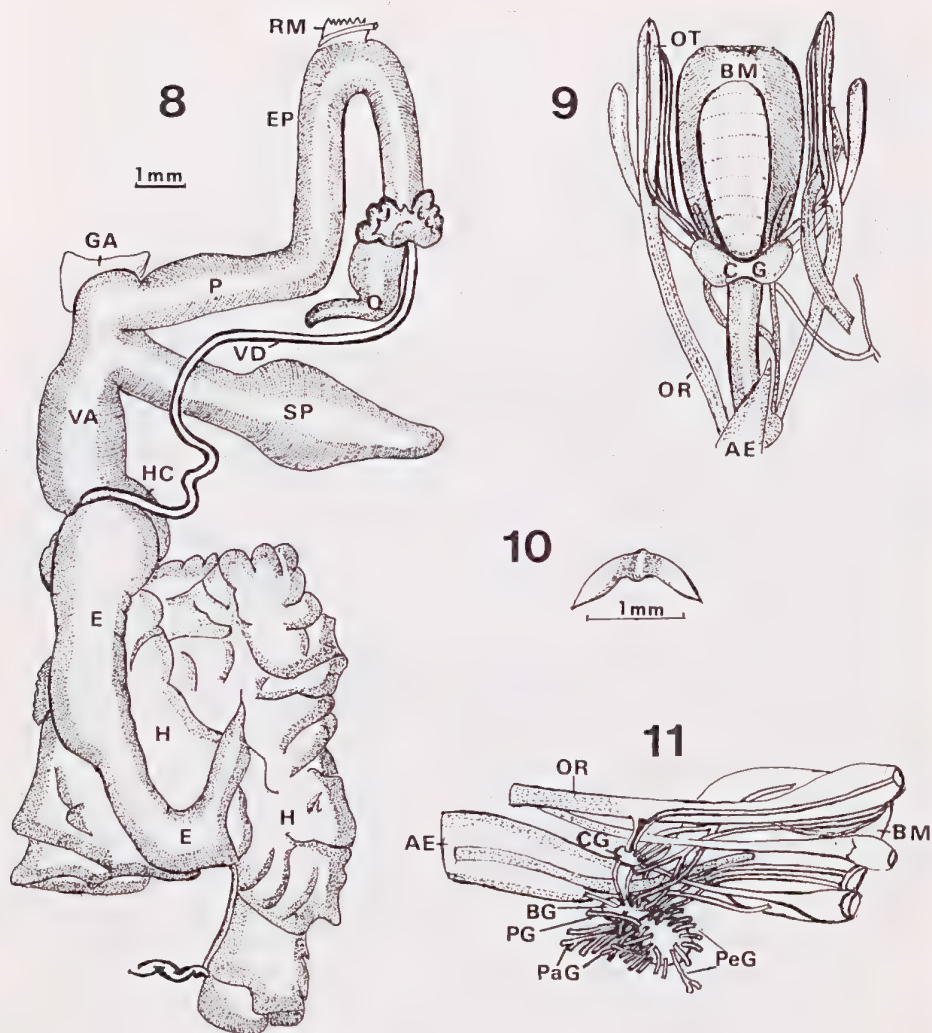
Hedley (1891) gave no specific locality with his description. Both Petterd and Dyer who assisted Hedley lived in northern Tasmania where black animals except for the yellow tail normally occur. Similar colouration has been observed in a south-west snail. The illustration of the genitalia bears some resemblance, the most significant difference being "the small round knob". The coil of the flagellum under low magnification could appear knob-like. Solem (1966) refers to such a feature in his sub-family description. This point was discussed with Dr. Solem but he could not recall its origin. He would not have overlooked Hedley's but Semper's (1885) figure shows a small knob at the tip of the elongate flagellum of his '*H. freycineti*'. Hedley's radular formula of 130 rows of 70.17.1.17.70 could suggest a northern animal if he counted the cusps of the marginals. The teeth illustrated are helicarionid but no northern animal studied to date fits the description. Black morphs occur in lower central Tasmania; it is possible he had one of these. Semper's (1885) description of *H. cuvieri* does not clarify the matter. *Helicarion* was known to past authors but only on a comparative basis; unfortunately the type species was not known with sufficient accuracy.

DISTRIBUTION

Helicarion cuvieri is here regarded as having a southern Tasmanian distribution. Study of some isolated morphs has not been completed but the species *sensu stricto* does not occur in northern or western regions nor on Bass Strait islands. Reports in the literature of mainland occurrences have not been proved. The habitat is rain forest to humid woodland, often below logs, although litter and moss are also favoured.

HELICARION FREYCINETI FERUSSAC

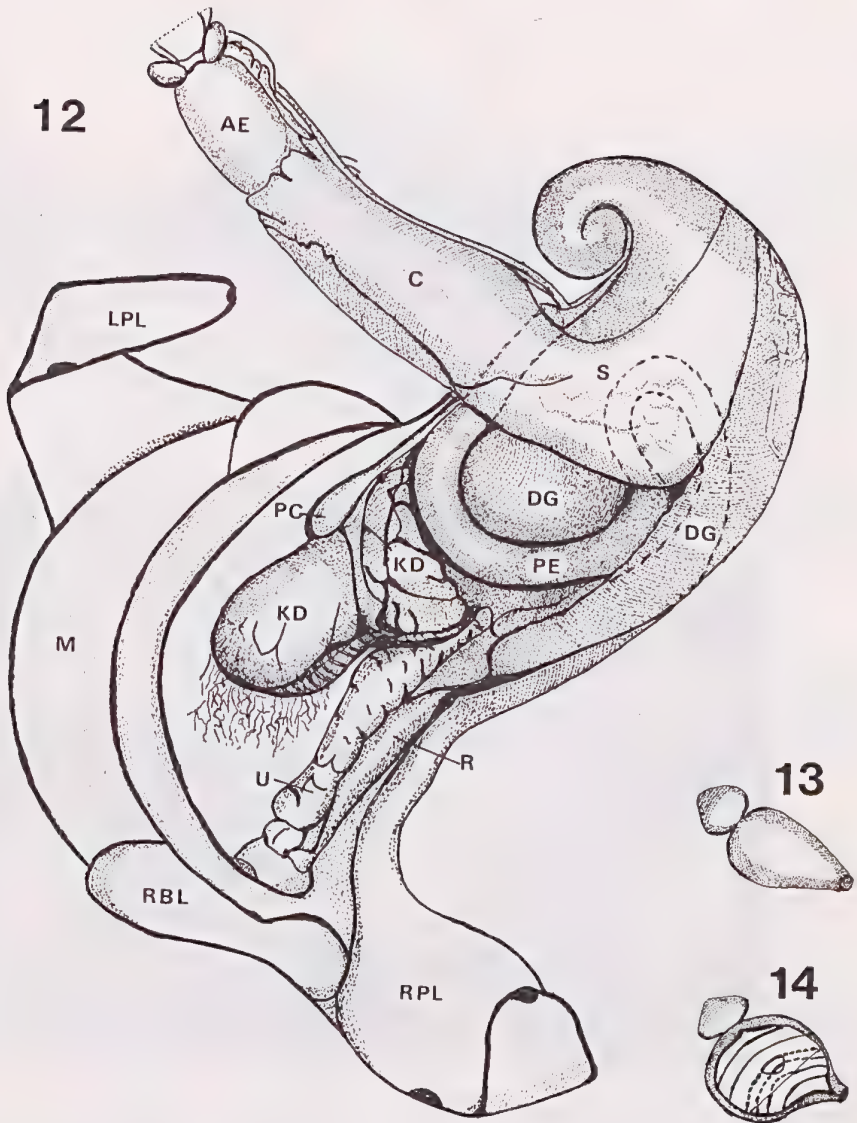
Syntypes from the Paris Museum were sent by M. Tillier. The three specimens proved to be from Botany Bay with the label 'Collect. Ferussac, 1837'. Enquiry for the type specimen was made at



FIGURES 8-11.

8. Detail of reproductive system, flagellum reversed
9. Buccal mass region, dorsal view.
10. Jaw.
11. Central nervous system, lateral view.

the same time as that for *H. cuvieri* and the above material, which was considered 'types' by Paris, all that could be accepted. M. Tillier wrote that the specimens "must be considered as syntypes, and you should select a lectotype among them." As Dr. Paget of Vienna wrote that there is no *Semper* material in his museum a lectotype was chosen as suggested. None of the Paris material is marked 'type' although two older labels were present. In addition two lots of animals sent were studied. One is labelled '*Vitrina freycineti* Fe. du Port Jackson Mss. Quoy et Gaimard 1819'. The genitalia had been removed. Probably collected during the Uranie voyage, it is not likely to have reached Paris



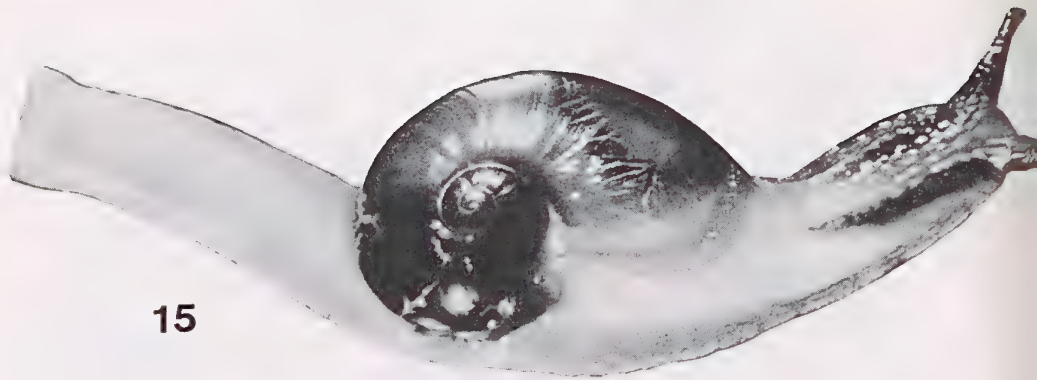
FIGURES 12-14.

12. Digestive system, dotted lines indicate location of oesophagus.

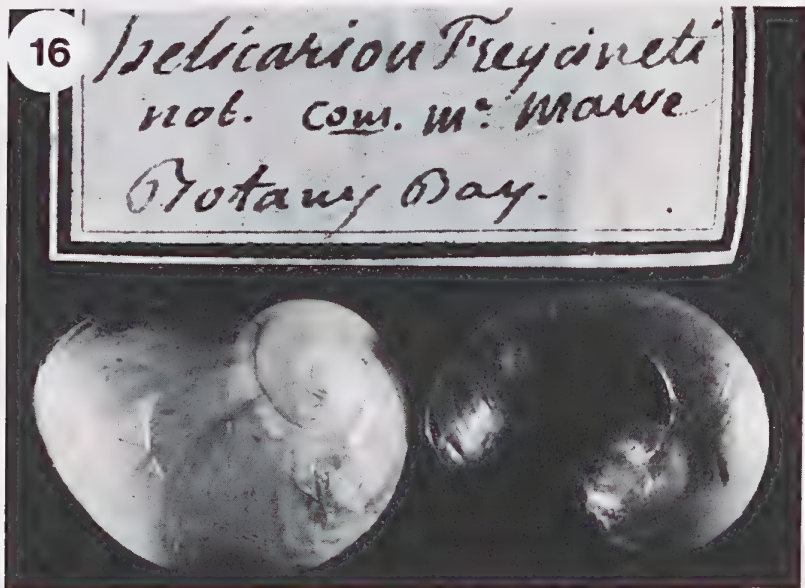
13. Heart, removed from pericardium.

14. Section through heart showing auricle internal detail.

in time for Ferussac's 1819 work. The second lot (two intact animals without shells) from Port Jackson were collected by Quoy and Gaimard; the label 'Exp^d. d'Urville 1829'. The three shells from Paris can be considered syntype material because they belonged to Ferussac's collection and were apparently of similar age to his described specimen. They came from an area close to the type locality. In the absence of other type material the largest shell is designated lectotype and the



15



16

FIGURES 15-16.

15. *Helicarion cuvieri* Ferussac, live animal.16. *Helicarion freycineti* Ferussac. Dorsal view of lectotype, ventral view of paralectotype.

remaining two paralectotypes. The animals, although collected in the type locality, are not of the same collection, but should be regarded as voucher material.

DESCRIPTIONS

HELICARION FREYCINETI FERUSSAC

Figure 16

1821. *Helicarion freycineti* Ferussac, *Hist. Moll.*, livr. 13, pl. 9a, f. 3,4.1821. . Ferussac, *Tabl. Syst. Limacons*, p. 24.

1825. *Helicolimax australasiae* de Blainville, *Man. Malac.*, p. 462.
 1825. *Vitrina freycineti* Gray, *Ann. Phil.*, 9: 408.
 1849. Pfeiffer, *Proc. Zool. Soc. Lond.* 1849: 132.
 1851. Woodward, *Man. Moll.*, p. 163.
 1855. Gray, *Cat. Pulm. Collt. Brit. Mus.*, 1: 67.
 1862. Reeve, *Conch. Icon.*, 13, pl. 6, f. 40, sp. 21.
 1868. Cox, *Mon. Aust. Land Shells*, p. 83, pl. 14, f. 7.
 1885. Semper, *Reis. im Philipp.*, 3: 31, pl. 3, pl. 6.
 1887. Fischer, *Man. de Conch.*, p. 459.
 1909. *Helicarion freycineti* Cox, *Alph. List Aust. Land Shells*, p. 31.
 1937. Iredale, *Aust. Zool.*, 9 (1) : 7.
 1941. *Vercularion freycineti* Iredale, *Aust. Nat.*, A1 (1) : 6.

DESCRIPTION BY FERUSSAC

"A species very close to *Vitrina monticola* Benson. It is more globular and with the spire a little more prominent. It is oval the spire barely convex, very short, formed of three whorls rapidly increasing, (re)united by a linear suture, simple and superficial. The last whorl is very big, depressed yet rather thick and convex at the periphery, wide below, a little depressed towards the centre. It ends in a very oblique aperture, very large, oval-oblong with elongated columella, thin regularly arched and accompanied by a membranous margin slightly slanted. The peristome is always thin, sharp, a little inverted inwards, convex in front, it is separated from the penultimate whorl by a not very deep angle. All the surface is smooth shining covered with ridges, rather large and increasing irregularly. This species is thicker and more solid than the majority of other species of the same genus. It is less transparent, its colour uniform, of a tawny yellow, fairly dark washed with green. The animal belongs to the genus *Helicarion* Ferussac, it is represented in this work violently contracted as result of having been submerged in liquid. Its foot is truncated and ends posteriorly in a large mucus crypt. This species is large, 19 mm long, 8 mm high."

DESCRIPTION OF LECTOTYPE

Shell (fig. 16) almost 3.5 whorls pale yellowish translucent, the last whorl descends slightly giving the spire a prominent aspect. The whorl slants slightly toward aperture, margin membranous but little evidence of inversion. Sculpture low irregular smooth ridges close shining, large near aperture, variable, radial weak irregular at periphery, crossed by extremely fine spiral striae. Shell not very thick or solid. Protoconch 2.25 whorls pale almost white, sculpture very weak radial lirae clearer at sutures, spiral striae barely visible.

DIMENSIONS	Diameter		Height	Aperture		No. of Whorls
	Maximum	Minimum		Height	Width	
Lectotype	16.5 mm	13.0 mm	9 mm	10.5 mm	11.0 mm	3.5 almost
Paralectotypes	14.6	11.5	7.0	10.4	9.4	3.5 almost
	14.8	11.5	8.4	9.0	9.5	3.4

Animal (collected by Quoy & Gaimard, Port Jackson, 1819) pale buff almost khaki, right pallial lappett thickened, rugose, 6 mm long, 3.5 mm wide, right body lappett with slightly elongated orange wart anteriorly, 2.5 mm wide below pneumostome, 7.0 mm long; left pallial lappett rounded 2.0 mm long, 1.5 mm wide curving across lip. Mantle about 3.0 mm long on neck, 6.5 mm wide. Foot sole tripartite, flat, 4.5 mm wide, central section tapering to foss, lateral margins 1.0 mm high to distinct peripodial groove, tail dorsally with distinct 2.5 mm keel to non-protruding caudal horn. Preserved animal bulky, 29 mm long 5.6 mm wide, anterior height 5.0 mm, at foss 3.5 mm, surface tubercular distinctly slanting posteriorly from hump, anteriorly sub-rounded, tubercles near verticle, lines of tubercles some broad 0.8 mm dorsal to 1.1 mm ventral width irregularly shaped, defined on tail, a distinct line slants forward below atrium; mantle surface rugose with small pustules. Tail 13 mm from base of viscera less than half the length. Kidney and albumen gland visible through visceral hump, the former pale cream, the latter pale orange. No wart is present in the other animals but mantle and lappetts are rugose in each case.

Iredale (1941) refers to reddish colour on the sides of the foot, but as such colours are sometimes unstable in preservative he may have had a fresh animal. Semper (1885) figures the genitalia. He shows the penis with a marked basal constriction, the flagellum very long with a small terminal knob. The bursa duct enters just anterior to the uterus remote from the atrium, the vagina straight not swollen. His figure of the teeth shows the rachidian mesocone long, slim and pointed, the

ectocones in the lateral teeth less pronounced. Iredale (1941) places *H. freycineti* in his genus *Vercularion*. This would be based on superficial characters, and as Semper had animals from Sydney and Cape York his description may be suspect on locality.

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VARIATION IN THE SEPIONS OF VICTORIAN CUTTLES (MOLLUSCA : CEPHALOPODA).

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SUMMARY

Data is presented on the variation found in beach stranded cuttle sepions from Victoria, Australia. It is found that the width - length relationship is the most useful enabling the determination for each species of juvenile - adult growth stages, sexual dimorphism and breeding cycles.

INTRODUCTION

Many of the described cuttle species from Australia are based on beach stranded sepions (Iredale 1926, 1954). Species have been separated from each other only on such tenuous grounds as being "wider", "thinner", "longer", "shorter", etc.; these differences being based on few, or even one specimen. Until the ranges of variability of the sepions are known for any species it is fruitless to propose new species on such grounds.

Until a rigorous research and collection programme is undertaken on the distribution and seasonal abundances of the live Sepiidae in Victorian waters we are restricted to observations on beach stranded sepions. From these specimens we must attempt to diagnose species, variation within species, sexual dimorphism within a species, growth rates and breeding cycles.

Detailed descriptions of the variations in length, width, thickness and striate zone length of the Victorian cuttles is presented.

The Victorian fauna of cuttles (Mollusca: Cephalopoda) consists of *Sepia apama* Gray, 1849, *S. braggi* Verco, 1907, *S. hedleyi* Berry, 1918, *S. novaehollandiae* Hoyle, 1909, *S. rex* (Iredale, 1926) (Bell and Plant 1977).

METHODS

The basic premise is that the number of specimens of all ages which are washed onto the beaches is in proportion to those animals living offshore.

The collection of large numbers of beach specimens from Collendina, Ocean Grove, Victoria was made at monthly intervals from July 1976 to July 1977. Two kilometres of beach was thoroughly searched from the seaward edge of the sand dunes to the waters edge (usually low water mark) and all complete and identifiable fragments of sepions were collected.

For all complete specimens the following measurements were made (in mm):

seption length - greatest length not including the spine if present,
 seption width maximum,
 seption thickness maximum,
 striate zone length - measured from the inside of any posterior shelf or outgrowth,
 spine length.

From these were calculated the width index - greatest width as a percentage of the seption length; similarly for a thickness index and a striate zone index.

For the plotted points in each graph a line of best fit was estimated by eye and drawn in.

RESULTS

Sepia apama Gray, 1849

The adult seption has been adequately described by Adam and Rees (1966) and especially well figured by McCoy (1889). However the juvenile seption has apparently not been described in detail.

The smallest juvenile seption found which can be safely identified as *apama* had a length of 5.2 mm. It is roundly triangular in outline, very flat both dorsally and ventrally, with a narrow chitinous margin. There are ten striae visible; the suture lines are ovate at the narrow posterior end but become more quadrate in shape at the anterior. Initially the seption must be almost circular but quickly changes (in 2-3 chambers) to a more quadrate shape. There is no indication of a spine on the smallest specimen but on a seption of $l = 8.9$ mm there is a very small raised boss whilst on septions of length $l = 11$ mm and greater there is a small bluntly rounded spine. The spine is present on specimens upto at least $l = 240$ mm but the posterior end of the seption is usually abraded in larger specimens. It is apparent that the spine grows with the outer cone as it becomes prolonged.

The thick V - shaped pad at the posterior edge of the hollow on the ventral side in the adults does not begin to appear in juveniles until about $l = 75$ mm. At this length the inner cone is beginning to thicken and fill the hollow below the inner cone platform. By length $l = 90$ mm the hollow has been filled and this part of the inner cone is forming thick limbs obscuring the earlier sutures; at this stage the two limbs may be completely fused together posteriorly and smoothly rounded or may be in the form of two slightly separated rounded lobes. There is no apparent change in the outer cone width or length upto $l \approx 90$ mm. At greater lengths the outer cone becomes wider and steeper sided with the thickened limbs of the inner cone becoming more pronounced. The outer part of the inner cone begins to cover the outer cone extensions at about $l = 110$ mm at which length the outer cone is very elongated. This inner cone covering is fused to the outer cone and by length $l = 180$ mm it covers over half the width of the outer cone at the posterior end but tapers anteriorly. The inner half of this fused inner cone shows a series of sub-parallel growth (?) lines.

(i) Length - width:

The width - length curve shows two relatively straight sections with a 'knee' at a length close to $l = 100$ mm. For $l < 100$ mm the points lie very close to the line but for $l > 100$ mm the spread of points is larger especially with greater length. Figure 2 shows the width index as a function of length. There is again a notable change in this index with length (i.e. with age) at $l = \pm 100$ mm. For these reasons, together with the growth changes discussed previously, the length of 100 mm has been taken as the dividing length between juvenile and adult septions. There is no evidence for sexual dimorphism at any stage of growth in these figures. However, when the relative frequency of each width index is found (fig. 3) the histogram is unimodal for $l < 100$ mm but bimodal for $l > 100$ mm. The maximum frequencies are at 47 - 48% for the juveniles and at 34 - 35% and 38 - 39% for the adults. It thus appears that dimorphism only occurs in adult specimens of *apama*. It is not known of course from the septions which of the maxima corresponds to the male or female animal.

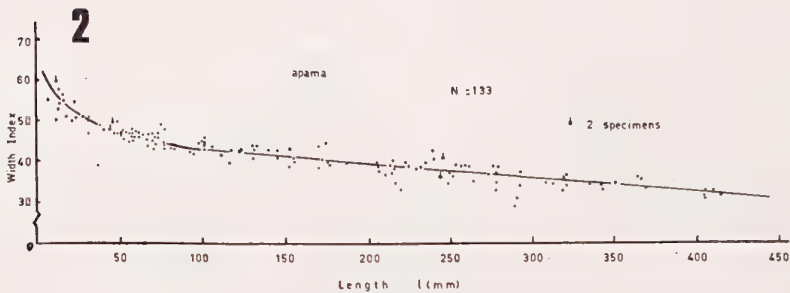
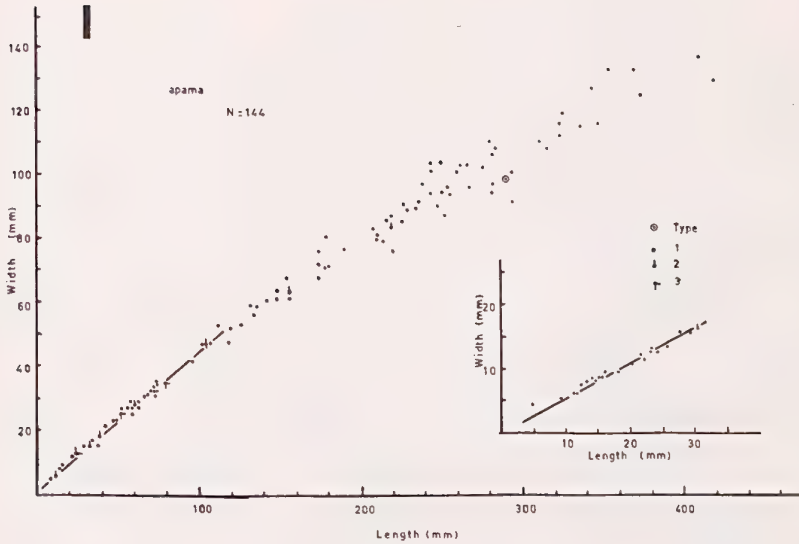
Specimens ranged in length from 6 to 420 mm.

(ii) Length - thickness :

The thickness index frequency curves show no evidence of dimorphism. Two - thirds of all specimens fall within the range 9.5 - 11.5% of the length (fig. 4). Juveniles have a prominent peak at 9.5 - 10% with adults at 11 - 11.5%.

(iii) Length - striate zone :

The striate zone index is quite variable with a range from 48% to 68% for adults with no



FIGURES 1-2.

1. *S. apama* : variation of width of sepium with length. Inset shows the smaller sepiions on a larger scale.
2. *S. apama* : variation in width index with sepium length.

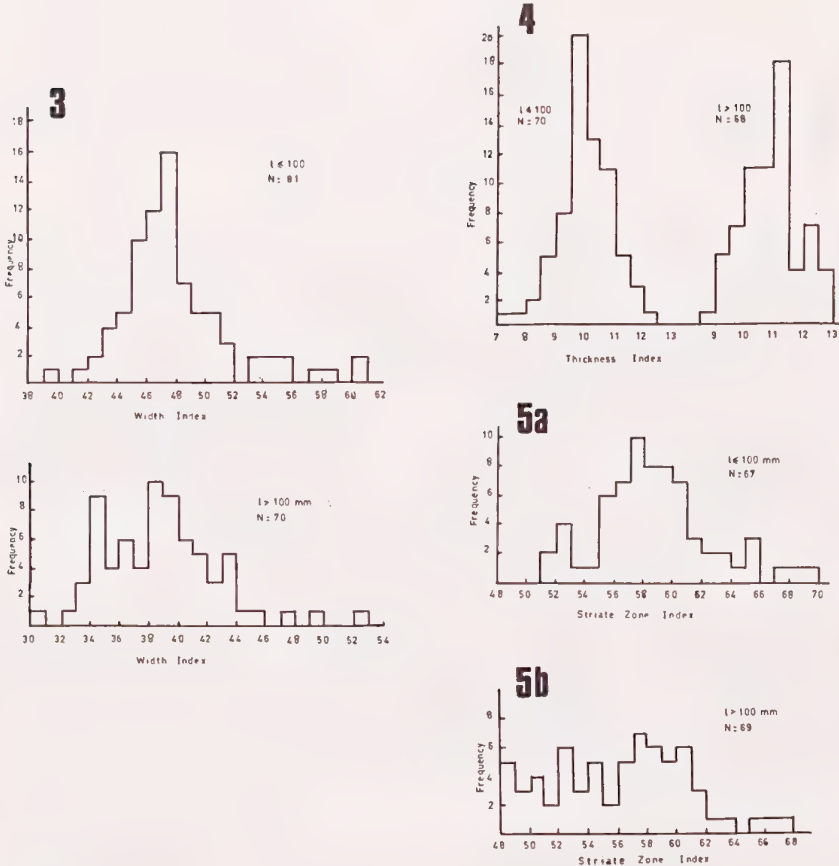
significant peak values. For the juveniles this index shows a wide spread of values with a peak from 56% to 61%. (Fig. 5).

Sepia braggi Verco, 1907

Sepions ranged in size from 6.5 mm to 66 mm. Small specimens were uncommon; the majority having lengths between 40 mm and 60 mm. This may be partly due to the fragile form of the juveniles and possibly to a different living habitat.

(i) Length - width :

The length - width curve (fig. 6) shows all specimens to lie, apart from the smallest, along a single growth line. The variation in width for a given length increases with greater length but



FIGURES 3-5.

3. *S. apama* : histograms of frequency of width index values.
 4. *S. apama* : histogram of frequency of thickness index values.
 5. *S. apama* : histogram of frequency of striate zone index values.

is not greater than 10%. The width index curve (fig 7) shows the characteristic shape of a rapidly falling curve initially and then a much slower growth change. The change in growth rate occurs at length $l = \pm 40$ mm. Indeed, for $l > 50$ mm the curve is almost horizontal. The sepiions only show variations of width index for $l > 40$ mm, so this length is taken as the juvenile - adult change length.

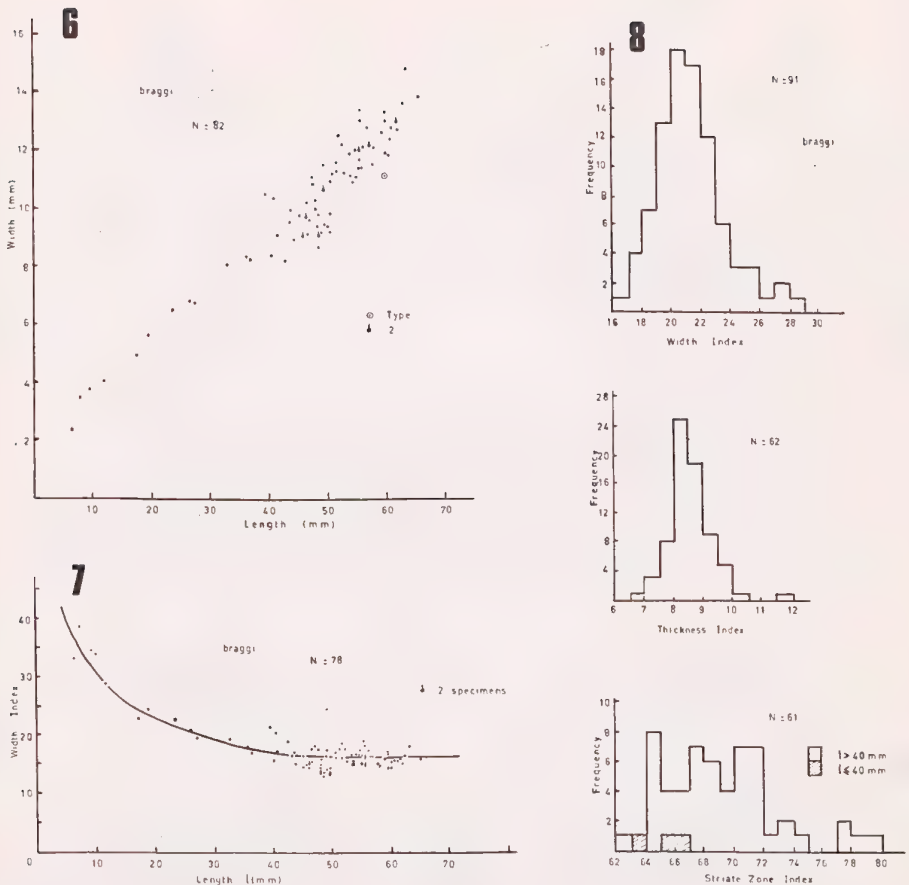
The histogram for width index (fig. 8) is unimodal with a maximum at 20 - 22%. There is no evidence for sexual dimorphism.

(ii) Length - thickness :

The thickness index (fig. 8) is strongly unimodal with the peak at 8 - 9%.

(iii) Length - striate zone :

Wide variation occurs in the length of the striate zone on the sepiions studied. The striate zone index (fig. 8) ranges from 50.8% to 79%. The four smallest sepiions, lengths 11.8, 23.8, 26.4 and 27.4 mm, had indices of 50.8, 53.4, 56.4 and 52.6% respectively. (These values are not shown on figure 8).



FIGURES 6-8.

6. *S. braggi* : variation in width of sepium with length.

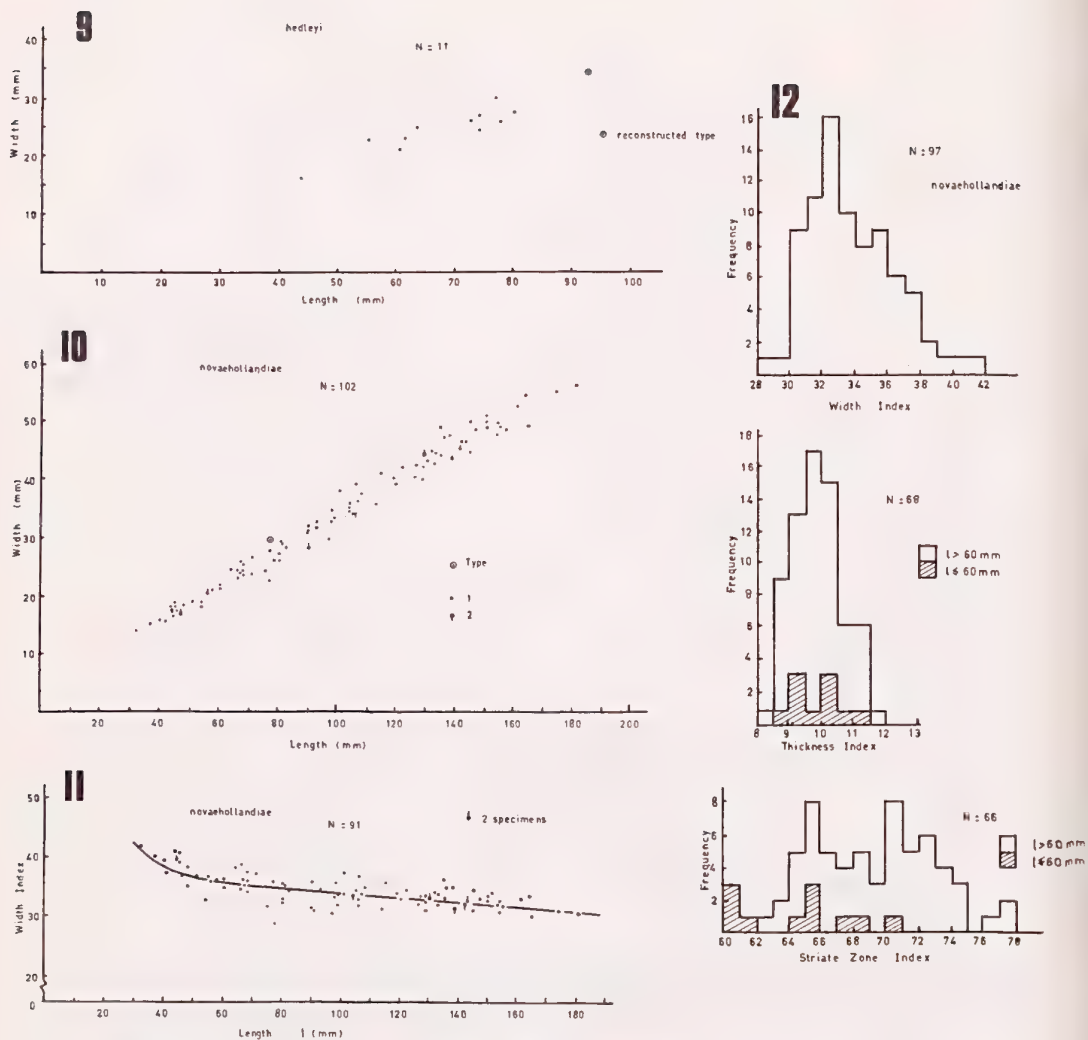
7. *S. braggi* : variation of width index with sepium length.

8. *S. braggi* : histograms of frequency of width index, thickness index and striate zone index values.

Sepia hedleyi Berry, 1918

Sepia of *hedleyi* are sparse on the Victorian coast. This is most likely due to their living habitat of deep waters upto at least 500 metre.

The sepium of *hedleyi* has not been adequately figured. The original figured by Berry (1918) was a reconstruction of a badly broken and dissolved sepium. Cotton and Godfrey (1940) gave a figure of a sepium they called *hedleyi* but Adam and Rees (1966) doubted that it was actually of *hedleyi*. In the N.M.V. collections there are live taken animals from Portland, Victoria, which agree with Berry's description of *hedleyi*; the sepiums of these specimens are closely similar to Berry's reconstructed sepium and are the same as that figured by Cotton and Godfrey. The figure of *hedleyi* given by Cotton (1929) is more acuminate anteriorly than any from the live animals but some of the beach stranded specimens are similarly shaped. From the sepiums of *hedleyi* seen (this collection, live taken animals and an extensive range from Merimbula, N.S.W.) the acuteness or otherwise of the anterior end is a quite variable character. Sepia ranged in length from 44 to 81 mm. Little can be deduced from such a small number of specimens but the width-length plot (fig. 9) shows that all points, including that of the reconstructed type, fall on a single straight line.



FIGURES 9-12.

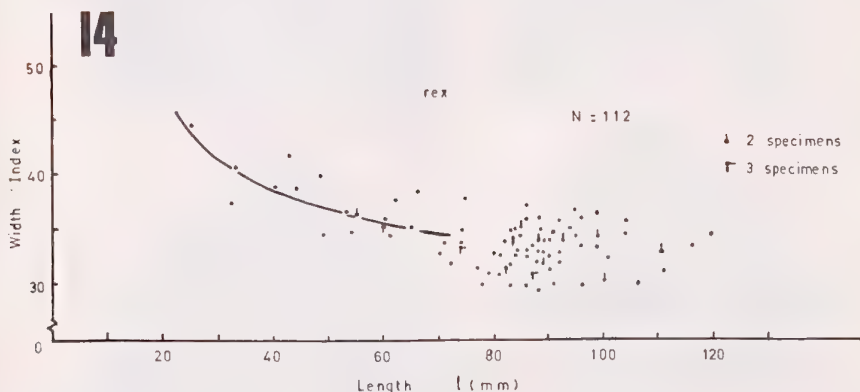
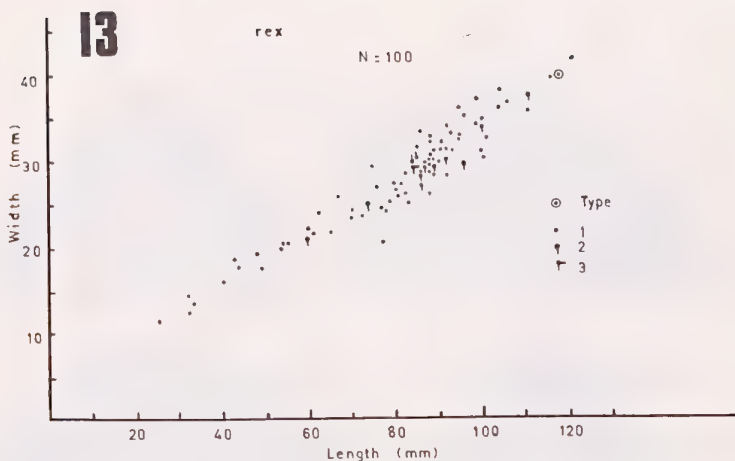
9. *S. hedleyi* : variation of width of sepiion with length.
 10. *S. novaehollandiae* : variation of width of sepiion with length.
 11. *S. novaehollandiae* : variation of width index with length.
 12. *S. novaehollandiae* : histograms of frequency of width index, thickness index and striate zone index values.

Sepia novaehollandiae Hoyle, 1909

(i) Length - width :

Sepions ranged in size from 40 to 180 mm. The length - width relationship remains constant over this range (fig. 10) with specimens only showing width variations for a given length for $l > 60$ mm. This length has been taken as representing the juvenile - adult length. As with other species the variations are greatest with increasing lengths.

The width index curve (fig. 11) shows the characteristic rapid decrease for juveniles ($l < 60$ mm) and then a slower more gradual decrease.



FIGURES 13-14.

13. *S. rex* : variation of width of sepium with length.14. *S. rex* : variation of width index with sepium length.

There is no evidence for dimorphism in the sepiens as the width index histogram (fig. 12) shows a unimodal curve with maximum frequency at 32 - 33%.

(ii) Length - thickness :

There is little variation in the relative thickness of the sepiens. The range is from 8.5 - 11.6% with a maximum number of specimens between 9.5 - 10% (fig. 12).

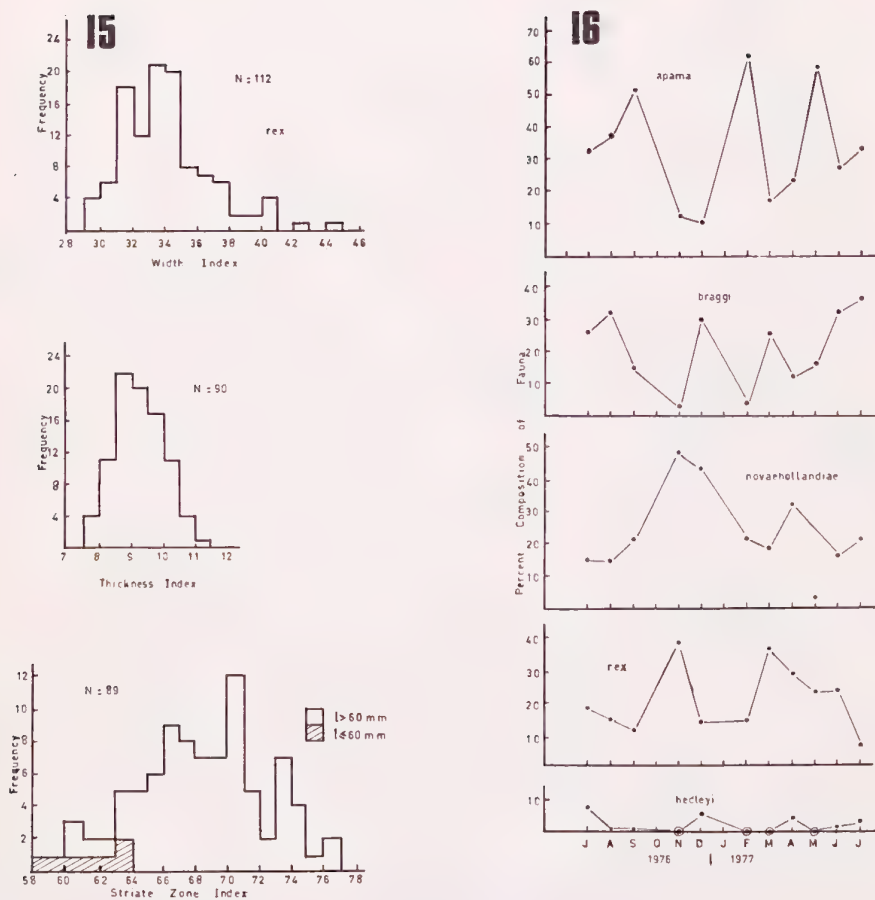
(iii) Length - striate zone :

The juveniles show a striate zone index peak of 64 - 65% while the adults show a bimodal pattern (fig. 12).

Sepia rex (Iredale, 1926)

(i) Length - width :

Sepiens ranged in length from 26 mm to 121 mm. This species shows the greatest spread in length - width relationship of all the species considered. (fig. 13, 14). Small specimens were uncommon but there is evidence that at length $l = 60$ mm the spread in width values for a given length becomes much greater. This length is thus taken as the length of juvenile to adult change. The width index histogram (fig. 15) is bimodal with maxima at 31 - 32% and 33 - 35%. *Sepia rex* therefore shows more pronounced dimorphism than any of the other species.



FIGURES 15-16.

15. *S. rex* : histograms of frequency of width index, thickness index, and striate zone index values.
 16. Variation in the faunal composition with date of collection.

FIGURES 17-27.

17-22. *Sepia apama*, showing the development of the posterior ventral thickening with increasing length. 17, $l = 56$ mm; 18, $l = 75$ mm; 19, $l = 96$ mm; 20, $l = 110$ mm; 21, $l = 156$ mm; 22, $l = 180$ mm.

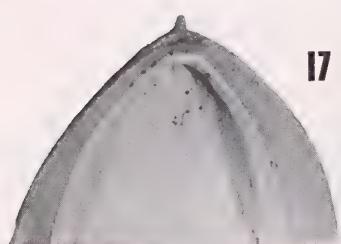
23. *Sepia apama*.

24. *Sepia novaeollandiae*.

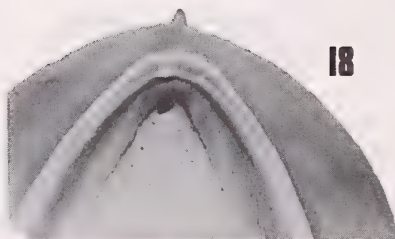
25. *Sepia hedleyi*.

26. *Sepia rex*.

27. *Sepia braggi*.



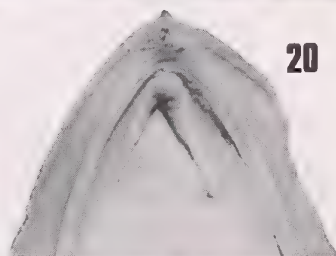
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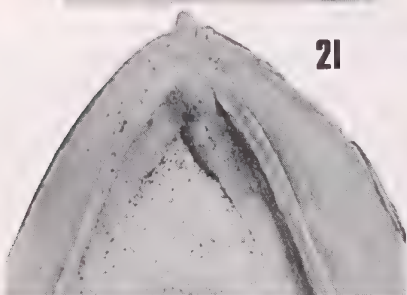
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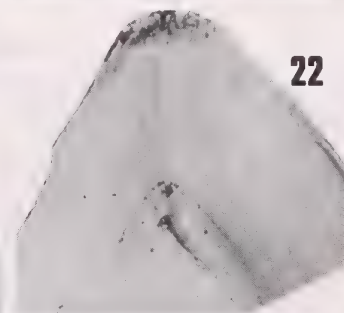
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26



27

(ii) Length-thickness :

The thickness index (fig. 15) is strongly unimodal with maximum at 8.5 - 9.5% with a range of 7.5 - 11.2%.

(iii) Length-striate zone :

This index shows a very wide range in adult specimens - from 60 to 77%. The juveniles have a much restricted range of 58 - 64% (fig. 15).

Faunal Variation with Time

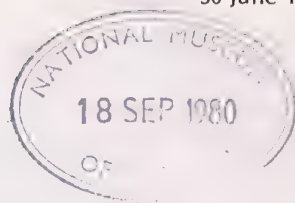
The overall variation in the faunal composition of the collected specimens is shown in fig. 16. Several points are of interest. Neglecting the variation in *hedleyi* as it is due to such few specimens taken, the other four species show pronounced variations over the 12 month period. Also, there is a clear inverse relationship between the presence of *apama* and *novaeollandiae*. It was at first thought that these faunal variations were due to the input of juveniles due to various cyclic breeding times. However, an analysis of the number of juveniles of *apama* present each month (the only species to have sufficient juveniles for analysis) shows this not to be the case as hatching of young occurred only once per year (Bell, 1979).

Discussion

This short study has shown that the sepiion variation within a species of cuttle is a function of the sepiion length i.e. a function of the age of the animal. The variation for a given age is rather restricted and where large e.g. *rex*, is most likely due to sexual dimorphism in the adult. In all species the juvenile animals give no indication of dimorphism. It is only after a certain length, taken here to represent the change from juvenile to adult, that any dimorphism or variability in the parameters measured becomes evident. Bearing this in mind it is thus possible to use the cuttle sepiions to characterize species.

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A revision of the Australian species of
Notoacmea, *Collisella* and *Patelloida*
(Mollusca : Gastropoda : Acmaeidae)

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ABSTRACT

The Australian species of *Notoacmea*, *Collisella* and *Patelloida* are revised on the basis of shell and radular characters. Six species are recognised in *Notoacmea*, two in *Collisella* and 12, together with two subspecies of an Indian Ocean species, in *Patelloida*. The majority of the species are found in temperate Australia, there being only 6 taxa recognised from tropical Australia. *Patelloida septiformis* Quoy & Gaimard, 1834 and *P. elongata* Quoy Gaimard, 1834 are both rejected from the Australian fauna.

INTRODUCTION

The Australian limpets of the family Acmaeidae have been reviewed by Oliver (1926) and Macpherson (1955), and the South Australian species by Cotton (1959).

Macpherson (1955) ignored a number of species and genera of the Acmaeidae but Oliver's (1926) revision is much more comprehensive.

Recent biological and ecological work on New South Wales limpets of the family Acmaeidae by one of us (R.G.C.) and independent observations by W.F.P. on Australian acmaeids and on type material have indicated that some of the conclusions reached by previous workers are unsatisfactory. No other Australian authors have had the opportunity to examine at first hand most of the type material, with the result that ignorance of the real identity of the types appears to have been the main factor which has given rise to misinterpretation.

The species of the genera *Notoacmea*, *Collisella* and *Patelloida* are revised herein. Another problematic genus, *Asteracmea* Oliver, 1926, a group possibly closely related to *Patelloida*, is not dealt with because of the lack of adequate material but is, nevertheless, greatly in need of revision. Oliver (1926) reviews the species of *Asteracmea* and separates the genus mainly on shell characters from *Patelloida*, the radula of the one species known being like that of *Patelloida*. The species of *Asteracmea*, if it is indeed a useful grouping, are small, often rather conical and usually have pink rays on the shell.

Two recent revisions by Christiaens (1975a, b) have appeared in a malacological society newsletter in which two new Australian subspecies were described and a new subgenus (of *Patelloida*) for an Australian species was proposed. The "publication" in which these names appeared barely meets the requirements of acceptability but nevertheless the two papers are a very useful compilation of information on the Acmaeidae, including as they do, a list of all named taxa. Several nomenclatural changes affecting Australian species are made by Christiaens, with many of which we agree. These are listed in the synonymies for the species included in this revision.

MATERIALS AND METHODS

The taxonomic decisions contained in this paper have been based on an examination of type specimens and other material mostly housed in The Australian Museum, Sydney. Field observations by one of us (R.G.C.) on New South Wales limpets encompass a much greater range of data than presented here, and will be the subject of additional publications.

Radulae were removed from specimens, cleaned in either potassium hydroxide or sodium hypochlorite, rinsed several times in distilled water, and mounted on aluminium stubs using double-sided sticking tape. Usually the radulae of at least two specimens from each lot were examined to check for variability. In most species the radulae of several lots covering the geographic range of the species were examined. When mounted, the radulae were coated with gold and examined under a Scanning Electron Microscope (S.E.M.). Photographs of both top and side views of the teeth were taken from a central region of the radula. All of these mounts, together with the specimens from which the radulae were removed, are located in The Australian Museum. Stub numbers cited refer to The Australian Museum S.E.M. stub collection and registration numbers cited in the figure captions refer, unless otherwise differentiated, to Australian Museum material.

Dimensions given include those for large specimens. This does not indicate the largest specimen seen, but is given as an indication of the upper end of the size range encountered in the species.

ABBREVIATIONS

- ANSP Academy of Natural Sciences of Philadelphia, Philadelphia.
 AMS The Australian Museum, Sydney.
 BMNH British Museum (Natural History), London.
 NHMB Museum für Naturkunde, Humboldt Universität, E. Berlin.
 NHMP Muséum National d'Histoire Naturelle, Paris.
 NMV National Museum of Victoria, Melbourne.
 SAM South Australian Museum, Adelaide.
 TM Tasmanian Museum, Hobart.

TAXONOMY

Family Acmaeidae Carpenter, 1857 (placed on the Official List of Family Names in Zoology, Opinion 344, ICZN, 1955).

Synonyms: Lottiidae Gray, 1840, *nomen oblitum*, Habe, 1944.

Tecturidae Gray, 1847, *nomen oblitum*.

Patelloididae Oliver, 1926.

Acmaeids can be distinguished from other limpet-like gastropods, by their simple, bilaterally symmetrical shell lacking any accessory apertures or slits, by the presence of a single bipectinate gill in a small anterior mantle cavity and by the radula which lacks any rachidian (central) teeth. Each half row of teeth has only 2* lateral teeth (one bicuspid, the other unicuspid, or with 3 separate teeth), and 0-2 marginal teeth. (See Fig. 1).

Keen (1960) reviewed the genera of the Acmaeidae and reduced all of the Australasian

genera to subgenera of *Acmaea* Eschscholtz, 1833. Oliver (1926) erected a useful classification based on the shell, gills and radula and proposed several new genera and subgenera. Oliver's classification is, we believe, a more meaningful interpretation of the genera of the Acmaeidae than Keen's and this view is supported by the findings of MacClintock (1967) in his study of the shell structure of the Patellacea. He showed that *A. mitra* Eschscholtz, the type species of *Acmaea*, is very distinct from other members of the Acmaeidae, although it resembles them in its radular and gill structure. He recommends restricting the usage of *Acmaea* to this species alone. McLean (1969) and McLean *in* Keen (1971), use several genera for the North American west coast Acmaeidae and other recent generic reviews (Moskalev, 1966, Golikov & Kussakin, 1972 and Christiaens, 1975a, 1975b) advocate the use of several genera.

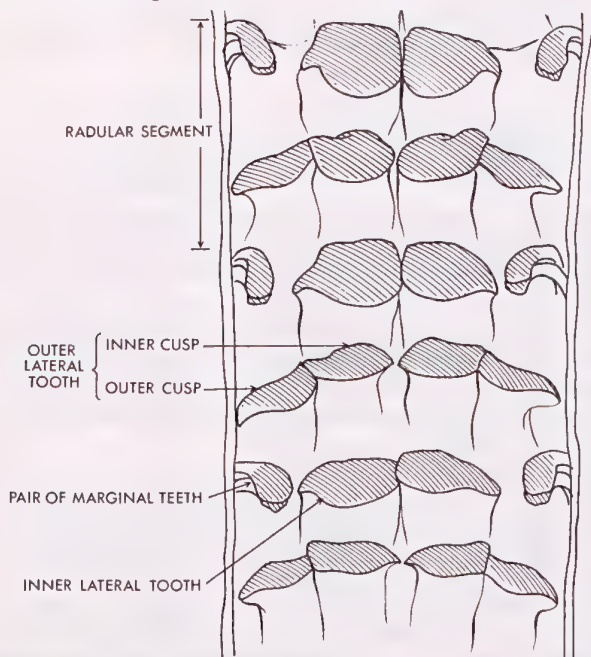


Figure 1. Generalized radula of *Patelloida* sp.

Christiaens (1975a, 1975b) reduces *Notoacmea* Iredale to a subgenus of *Collisella* Dall and also includes as subgenera (of *Collisella*) *Naccula* Iredale, 1924 and *Simplacmaea* Christiaens, 1975 (a). Although we regard *Notoacmea* as a full genus, we concede that the shells of *Collisella* species and *Notoacmea* species are very similar. The same is true, however, for shells of species of *Patelloida* Quoy & Gaimard which Christiaens (1975b) maintains as a distinct genus. The loss of one of the two pairs of marginal teeth seen in *Patelloida* gives rise to the *Collisella* condition and the loss of both pairs of marginal teeth to the condition seen in *Notoacmea*. This reduction phenomenon probably occurred more than once during the evolution of the group. Because of the greatly different shell characters between *Naccula/Simplacmaea* and *Notoacmea*, these groups are not considered here to be congeneric and the similarity in their radular formulae is interpreted as resulting from convergence.

The family names listed in the synonymy above have all been employed by recent

* Foot note: Several authors regard the acmaeid lateral teeth as consisting of three teeth in all genera. This is probably true but the two outer teeth are more-or-less fused and are more conveniently regarded as a single tooth in the genera under consideration.

workers. Two are interpreted as *nomina oblita* but this matter probably requires a ruling by the ICZN to achieve stability.

The diagnoses presented for each species attempt to cover the normal range of variation in both shell and radular features but do not allow for the occasional "freak" specimen.

Key to Genera

- Radula with 2 marginal teeth
(2-2-0-2-2) *Patelloida*
- Radula with 1 marginal tooth
(1-2-0-2-1) *Collisella*
- Radula with no marginal teeth
(0-2-0-2-0) *Notoacmea*

Genus **Notoacmea** Iredale, 1915.

Type species (original designation): *Patelloida pileopsis* Quoy & Gaimard, 1834.

Synonyms. *Parvacmea* Iredale, 1915. Type species (original designation): *Acmaea daedala* Suter, 1907. *Conacmea* Oliver, 1926. Type species (original designation): *Acmaea parviconoidea* Suter, 1907. ?*Subacmea* Oliver, 1926. Type species (original designation): *Notoacmea (Subacmea) scopulina* Oliver, 1926.

The Australian species in this genus have previously been reviewed by Oliver (1926) and Macpherson (1955). Oliver (1926) used 4 subgenera (other than the typical subgenus) for the Australasian species of *Notoacmea*. We can see no justification in using subgenera for any of the Australian species as the subgeneric characters utilized by Oliver appear to us to be of specific importance only.

MacClintock (1967) examined the shell structure of *N. pileopsis*, *N. parviconoidea* (Suter) (the type species of *Conacmea* Oliver), *N. fragilis* (Sowerby) (the New Zealand type species of *Atalacmea* Iredale), *N. "subundulata" Angas* (possibly *N. alta* Oliver), and *N. "septiformis" Quoy & Gaimard* (= *N. flammea* (Quoy & Gaimard) herein). These species fall into two closely related groups (MacClintock's groups 4 and 5). *N. scopulina* Oliver, the type species of *Subacmea* Oliver, was placed by MacClintock in his group 1. This may be a result of a misidentification or, possibly, *Subacmea* represents a group separately derived from *Patelloida* (several species of which are represented in MacClintock's group 1) by the loss of the marginal teeth of the radula. The type species of *Radiacmea*, *Acmaea cingulata* Hutton (= *inconspicua* Gray) is also placed in group 1 by MacClintock, suggesting a possible close relationship between *Subacmea* and *Radiacmea* as both groups lack marginal teeth.

Notoacmea alta Oliver, 1926. Pl. 1, figs 1-5, pl. 9, figs 1-4.

Acmaea conoidea. — (?) Angas, 1865: 186; (?) Tate, 1897: 43; Pritchard & Gatliff, 1903: 193 (in part, non Quoy & Gaimard, 1834).

Notoacmea (Conacmea) corrosa Oliver, 1926: 578, pl. 99, fig. 5, text fig. G.

Notoacmea (Conacmea) alta Oliver, 1926: 579, pl. 99, fig. 6.

Notoacmea alta. — Macpherson, 1955: 255, fig. in text, pl. 19, figs 3, 4 (radula); Macpherson & Gabriel, 1962: 54, fig. 73.

Collisella (Parvacmea) corrosa. — Christiaens, 1975b: 105.

Collisella (Parvacmea) alta. — Christiaens, 1975b: 105.

Diagnosis. *Shell* (pl. 1, figs 1-5). Thin, depressed conical to acutely conical, with apex anterior to almost central. Anterior slope straight or slightly convex. Surface of shell almost smooth, with extremely close and fine radial and concentric striae. Colour is generally dark grey/brown to black, sometimes with a variable pattern of white radial markings. Interior of shell is either completely black, or has a dark band around the margin.

Radula (pl. 9, figs 1-4). Inner cusp of outer lateral teeth of approximately same length as those of inner lateral teeth, both rather long and narrowly triangular. Outer cusps of outer lateral teeth slightly less than half size of inner cusps, triangular in shape. Inner lateral teeth have long bases; outer lateral teeth short ones. Radular segment fractionally longer than broad.

Dimensions

	Height	Length	Width
Holotype of <i>N. alta</i>	4mm	6mm	5mm
Holotype of <i>N. corrosa</i>	5.0	8.5	6.5

Types. *N. alta*. Holotype, AMS, C105731, South Australia (pl. 1, figs 1-3).

N. corrosa. Holotype, AMS, C.105730. Blackmans Bay, Derwent Estuary, Tasmania (pl. 1, figs 4, 5).

Distribution. Southern Australia from Spencer Gulf, South Australia to Nadgee, southern New South Wales and the east coast of Tasmania. Found in fairly protected areas of the mid-littoral, often on the shells of bivalves (especially *Brachidontes rostratus*) or gastropods.

Remarks. Several of the earlier records of this species were misidentified as *Acmaea conoidea* (Q. & G.). Oliver (1926) realised that the species found in southern Australia and Victoria were not conspecific with *conoidea* and he renamed it *N. alta*, whereas the species referred to as *conoidea* in Tasmania he called *N. corrosa*. Macpherson (1955) recorded *N. alta* from Bass Strait, Victoria and from eastern South Australia but did not mention any Tasmanian records, nor did she refer to *N. corrosa* Oliver or "*Acmaea*" *conoidea* (Q. & G.).

An examination of the type of *conoidea* from King George Sound showed it to be a distinct species from *alta* (see below) but specimens of *N. corrosa* from Tasmania were identical to *N. alta*. The type of *N. alta* is a shell in good condition but is localised simply as "South Australia" and was the only specimen seen by Oliver. This specimen presumably contained a dried animal because Oliver described the radula. The type of *N. corrosa* is an eroded shell and Oliver provided a figure of the radula. The description of *N. corrosa*, precedes that of *N. alta* but the name *alta* has become established in the literature so, as the first revisers, we select the name *Notoacmea alta* Oliver for this species.

Cotton (1959) places *N. alta* in the synonymy of *Conacmea subundulata* (Angas) because of an apparent misinterpretation of the type material of *subundulata* by Verco. Verco's (1906) records of this species include two sublittoral localities which are an unlikely habitat for this species and appear to refer to a form of *Collisella mixta* (Reeve) or *Notoacmea flammea*, of which *Acmaea subundulata* Angas is a synonym. Material in the AMS presented by Verco with the name *subundulata* from 'St. Vincent Gulf' consists of 2 specimens of a high-spired form of *N. flammea* and 1 specimen of *Collisella* cf. *mixta*. Another lot (ex Verco) in the NMV from Denial Bay, South Australia, is *N. alta*. Cotton's (1959) figure of the radula of "*subundulata*" is a copy of Torr's (1914) figure.

Several temperate Australian species attain a tall, conical shape and are frequently confused. These include *Collisella mixta*, *Notoacmea flammea*, *N. corrodenda* (May), *N. conoidea*, *Patelloida mufria* (Hedley) and *P. insignis* (Menke). It is, unfortunately, often extremely difficult to separate these species on shell characters alone, especially when dealing with eroded specimens.

Notoacmea (?) conoidea (Quoy & Gaimard, 1834). Pl. 1, figs 6-11.

Patelloida conoidea Quoy & Gaimard, 1834: 355, pl. 71, figs 5-7.

Chiazacmea flammea conoidea. — Oliver, 1926: 560 (in part).

Diagnosis. Shell (pl. 1, figs 6-11). Of moderate size for family, usually tall-spined (often nearly as high as long) with narrow dark-brown radial lines on a greyish-brown to whitish background. Internal margin with brown spots corresponding to external colour lines.

Radula. Not known from material definitely attributable to this species but small specimens tentatively identified as *N. conoidea* have a radula similar to that of *N. alta*.

Dimensions

	Height	Length	Width
Holotype	11.40mm	13.74mm	11.32mm
Figured specimen (King George Sound)	9.50	13.16	10.05

Holotype. The specimen figured by Quoy & Gaimard, NHMP (pl. 1, figs. 6-8); King George Sound, south Western Australia. Another shell together with the holotype is a specimen of *Collisella onychitis* (Menke), but as Quoy & Gaimard state that they had only one example of their *P. conoidea* this cannot be regarded as part of the type series.

Distribution. Rottneest Island (?) to King George Sound, south Western Australia. Shallow sublittoral (?) in sheltered areas.

Remarks. The holotype of *P. conoidea* is a large, eroded shell lacking a distinct external colour pattern (due to erosion of the surface) but has, on the margin of the shell, numerous brown spots suggesting that the younger shell may have had brown radial bands externally. A few specimens (shells only) from south Western Australia (including King George Sound) agree rather well with this specimen. This species differs from *Patelloida insignis* (Menke), with which it is sympatric, in that specimens are very tall spired, with equally prominent, narrow radial colour bands and finer external radial striae.

Oliver (1926) interpreted *N. conoidea* as a Western Australian subspecies of *flammea* auct. (= *Patelloida insignis* (Menke)) but the radulae of two small specimens, possibly referable to *conoidea*, were examined and found to be similar to that of *Notoacmaea alta*. Unfortunately no topotypic or adult material is available for the examination of radulae, so there does remain a possibility that the lectotype of *conoidea* may be a high-spired variant of *P. insignis* (Menke) and that the other material examined (consisting of specimens smaller than the lectotype) may be a south Western Australian form of *N. alta*.

A few high-spired shells from Rottneest Island, Western Australia, are similar to this species but show a weakly defined 'Maltese Cross' marked on the shell and so may be a high-spired form of *Patelloida insignis*.

Notoacmaea corrodenda (May, 1920). Pl. 1, figs 12-14, pl. 11, fig. 3.

Patelloida corrodenda May, 1920: 66, pl. 17, fig. 24.

Notoacmaea (*Subacmaea*) *corrodenda*. — Oliver, 1926: 581.

Collisella (*Parvacmaea*) *corrodenda*. — Christiaens, 1975b: 105.

Diagnosis. *Shell* (Pl. 1, figs 12-14). Small, rather solid, ovate and usually flattened. Sculptured with several low, narrow ribs. Apex at about anterior 1/3. Posterior slope slightly convex, anterior slope slightly concave. Ribs white or cream in colour, interspaces dark-brown. Interior of shell shows external pattern around margin, remainder dirty white to grey or pale-brown, spatula usually with dark-brown middle area and white border.

Radula (pl. 11, fig. 3). Inner lateral teeth broad, cusps long and pointed with medium-sized bases. Inner cusps of outer lateral teeth broad and approximately $\frac{3}{4}$ of the length of those of inner lateral teeth; outer cusps small and triangular in shape. Outer lateral teeth have short bases. Radular segment much longer than broad.

Dimensions

	Height	Length	Width
From original description	5mm	14mm	11mm
Lectotype	4.70	15.20	11.65
Paralectotype	4.9	14.3	12.0
Figured paralectotype	4.54	13.57	10.7
Average specimen (South Tasmania)	4.3	13.5	10.4
Large specimen (Frederick Henry Bay, Tasmania, ex May Colln, SAM)	7.52	18.85	14.86

Types. Lectotype (here chosen) and paralectotype, TM, E334/7675, C1709, 2 paralectotypes, AMS, C45952 (pl. 1, figs 12-14), 19 possible paralectotypes, May Collection (No. 363) SAM; western shore of Frederick Henry Bay, Tasmania.

Distribution. Tasmania, Bass trait and western Victoria, on rocks in lower littoral.

Remarks. Macpherson (1955) omitted this species from her revision. The radula indicates that it belongs to the genus *Notoacmea* as shown by Oliver (1926). It is distinguished from all other species of the genus by the prominent, white or pale radial ribs on the dark shell. This species has not previously been recorded from Victoria.

Notoacmea flammea (Quoy & Gaimard, 1834). Pl. 2, figs 1-18, pl. 9, figs 5-10.

Patelloida flammea Quoy & Gaimard, 1834: 354, pl. 71, figs 15-24.

+ *Acmaea scabrillirata* Angas, 1865: 154.

? *Acmaea subundulata* Angas, 1865: 155; Oliver, 1926: 573.

? *Patella* sp. Maplestone, 1872: 51, pl. 27, fig. 21 (radula).

Acmaea subundulata. — Verco, 1906: 215 (in part); Torr, 1914: 366, pl. 20, fig. 10 (radula).

Acmaea septiformis. — Verco, 1906: 215; Torr, 1914: 366, pl. 20, fig. 9 (radula) (non Quoy & Gaimard, 1834).

✓ *Notoacmea flammea diminuta* Iredale, 1924: 235.

+ *Notoacmea* (*Notoacmea*) *septiformis*. — Oliver, 1926: 572 (non Quoy & Gaimard, 1834).

Notoacmea (*Notoacmea*) *septiformis scabrillirata*. — Oliver, 1926: 573.

- *Notoacmea septiformis scabrillirata*. — Macpherson, 1955: 254, fig. in text, pl. 19, figs 1, 2 (radula).

Notoacmea septiformis. — Cotton, 1959: 317, fig. 213.

Notoacmea scabrillirata. — Cotton, 1959: 318, fig. 215; Macpherson and Gabriel, 1962: 54, fig. 72.

Conacmea subundulata. — Cotton, 1959: 319, fig. 215 (in part).

Diagnosis. Shell (pl. 2, figs 1-18). Small, thin and flattened to conical, with apex markedly anterior to slightly anterior. Anterior slope slightly concave, posterior slope gently convex. Surface usually sculptured with rather widely-spaced, minutely-granular, fine radial striae. The colour is cream to black overlain with a variable, reticulate or radial pattern of brown or black. Exterior pattern usually shows through to interior, especially at the margin. Interior usually pale, with white to bluish inside outer rim in adult.

Radula (pl. 9, figs 5-10). Inner lateral teeth and inner cusps of outer lateral teeth both very long, narrow and pointed. Outer cusp of outer lateral teeth very small and triangular. Radular segment longer than broad.

Dimensions

	Height	Length	Width
Lectotype of <i>P. flammea</i>	4.00mm	11.25mm	9.60mm
Paralectotypes of <i>P. flammea</i>	4.21	11.16	9.39
	2.30	9.20	7.76
	3.12	10.24	8.26
	3.37	9.06	7.00
	3.5 (approx)	10.90 (approx)	8.70
Holotype of <i>A. subundulata</i>	5.70	14.75	11.70
Large specimen (Port Phillip Bay, Victoria)	5.00	16.96	14.28
Large specimen (Sydney)	4.26	13.85	11.00
Conical specimen (Oyster Cove, Tasmania)	5.95	9.70	8.71
Large specimen (Oyster Cove, Tasmania)	6.50	15.91	14.00

Types. *P. flammea*. Lectotype (here chosen) (pl. 2, figs 1-3) and 5 paralectotypes (pl. 2, figs 4-12), NHMP, Hobart, Tasmania. *A. scabrillirata*. Not found; "Port Lincoln, Hobsons Bay". Two lots in the BMNH are from New South Wales ex Angas (BMNH, 70.10.26.157; 1900.2.8.19). Neither of these lots are types. *A. subundulata*. Holotype (pl. 2, figs 13-15), BMNH, 71.7.8.9. Port Lincoln, South Australia. *N. flammea diminuta*. Not found; Sydney.

One lot of 17 specimens in the AMS (C.49539) has a note in Iredale's hand giving his name and the word "topotypes". These are from Bottle and Glass Rocks, Sydney, New South Wales and were collected by Iredale in August, 1923 (pl. 2, figs 16-18).

Distribution. Southern Australia from Perth in Western Australia to Sydney in New South Wales and throughout Tasmania. Found in protected areas of the lower littoral, often on the sides of, or underneath, boulders.

Remarks. The 6 specimens here regarded as syntypes of *Patelloida flammea* Quoy & Gaimard prove to be conspecific with the species usually known as *A. scabrilirata*, the shells agreeing in every important character. Specimens in the syntype series agree rather well with Quoy & Gaimard's figures 17-20, but it has not been possible to match precisely the figures with any specimens in the syntype series. The similarities with figures 17-20 are, however, very close and the specimens could include those illustrated. In order to stabilise the name a lectotype has been chosen above from the syntype series.

Iredale (1924) came closest to correctly interpreting *flammea* by regarding it as the "eastern representative of Quoy's own *septiformis*". His subspecies *flammea diminuta*, which is also assumed to be a synonym of *A. scabrilirata*, also indicates that he interpreted Quoy and Gaimard's *flammea* as we have done. Most other Australian authors have, however, misidentified *flammea* as the species here referred to as *Patelloida insignis* (Menke). Hedley (1915) stated that *Patelloida flammea* "is a compound of two species, one of which occurred on the beach at Hobart, and the other at the Island of Guam". He advocates the use of the name *Patella mixta* Reeve for *flammea* auct. and restricts the use of *flammea* to the Guam species. Iredale (1924) and Oliver (1926) disagree with this conclusion, pointing out that Quoy & Gaimard selected the Tasmanian shell as the typical one. Angas described the beaded ribs on the shell of *A. scabrilirata* so that there is little doubt that his species is *flammea* in our sense.

Although usually associated with *N. scabrilirata*, *P. septiformis* Quoy & Gaimard, 1834 is, as shown below, apparently not an Australian species.

The type specimen of *A. subundulata* (pl. 2, figs 13-15) is a whitish, flat, rather thickened shell showing little external or internal colour. Other specimens from South Australia in the BMNH and some from Tasmania in the AMS are very similar and appear to be varieties of *N. flammea* with which they intergrade. Verco's (1906) and Cotton's (1959) interpretations of *subundulata* appear to refer to a compound of *Notoacmea alta*, *N. flammea* and *Collisella* cf *mixta* as indicated above.

High-spined specimens of *N. flammea* have been variously referred to *conoidea*, *alta* etc., but can be distinguished by the characteristic fine, rather widely-spaced, beaded riblets forming the exterior sculpture of *N. flammea*. High-spined shells tend to be more typical of specimens living in the open whereas the typical, flattened form generally lives beneath stones.

Adam & LeLoup (1938) recorded a species of *Patelloida* from New Guinea as *Acmaea flammea*. Their specimens have nothing to do with *N. flammea* and it is unclear as to which species of *Patelloida* their specimens should be assigned.

Notoacmea mayi (May, 1923). Plate 3, figs 1-3.

Acmaea cantharus. — T. Woods, 1877: 45; Iredale, 1915: 429 (*non* Reeve, 1855).

Patelloida mayi (Iredale MS) May, 1923: 100, pl. 22, fig. 33.

Notoacmea mayi. — Iredale, 1924: 235; Singleton, 1937: 390; Macpherson, 1955: 253, figs in text, pl. 18, figs 1, 2 (radula); Macpherson & Gabriel, 1962: 53, fig. 70, a.

Notoacmea (*Notoacmea*) *mayi*. — Oliver, 1926: 571.

Collisella (*Notoacmea*) *mayi* — Christiaens, 1975b: 103.

Diagnosis. *Shell* (pl. 3, figs 1-3). Rather thick and of low profile; apex at anterior margin, often extending beyond the margin; anterior slope steep, posterior slope convex; surface lacking radial sculpture. Usually uniform light brown to grey, but may be mottled with

darker greys or browns. Interior dark with spatula white to brown or black, with a band of grey-white inside the black or spotted (black and yellow) margin.

Radula. Inner lateral teeth long and pointed. Outer lateral teeth with inner cusps much larger and more rounded than outer cusps. Both teeth have short bases. Radular segment is considerably longer than broad (after Macpherson, 1955).

Dimensions

	Height	Length	Width
Lectotype	4.55mm	23.10mm	18.75mm
Paralectotypes	4.00	17.17	13.36
	5.50	18.54	14.21
	6.62	26.10	21.16
Large specimen (Port Arthur, Tasmania)	7.7	25.8	21.0

Type. Lectotype (here chosen) (pl. 3, figs 1-3), May Colln (no. 399A), SAM, D16191; with 7 + 5 paralectotypes (399, 399A) SAM, D16192, D16193: Frederick Henry Bay, Tasmania. Originally given as "south of Tasmania, rocks at half tide".

Distribution. Eastern South Australia, western Victoria and Tasmania. Found on rock vertical faces in the upper littoral.

Remarks. This species is one of the most distinctive limpets in Australia, the marginal or submarginal apex being very characteristic. It is closely related to *N. petterdi* with which it overlaps in both range and habitat, but can be distinguished by the position of the apex and the lack of radial sculpture.

The name *cantharus* Reeve was used for this species by early workers but Iredale (1915) considered Reeve's species to be conspecific with *Notoacmea pileopsis* (Quoy & Gaimard) from New Zealand. Christiaens (1975b : 103) has indicated that he believes *cantharus* and *mayi* to be conspecific but we do not concur with his conclusion. One of us (W.F.P.) has examined the types of *Patella cantharus* in the British Museum and agrees with Iredale's conclusion.

When May (1923) introduced Iredale's manuscript name for this species he simply stated in an appendix "From comparison with the type in the British Museum, our shell appears not to be *cantharus*. Iredale proposes to give it the name *mayi*". May refers to a figure and the caption to that figure states "apex at the margin". This descriptive statement together with the figure is sufficient to introduce the name. The phrase "our shell" is here interpreted as the shells that May had before him, although it could be argued that he may have been referring to the Tasmanian "shell" as contrasted with *cantharus* Reeve. Thirteen specimens in 2 lots in the May collection in the SAM bear the name *mayi* Iredale in May's handwriting and are here regarded as syntypes. One of these specimens is here designated as lectotype (pl. 3, figs 1-3). May's illustration is said to be half size which would give the figured shell a total length of 28.4mm. No specimens of *mayi* available to us reach this length.

Notoacmea petterdi (T. Woods, 1876). Pl. 3, figs 4-6, pl. 10, figs 1, 2.

Acmaea petterdi T. Woods, 1876: 155.

Notoacmea (Notoacmea) petterdi. — Oliver, 1926: 574.

Notoacmea petterdi. — Macpherson, 1955: 254, figs in text, pl. 18, figs 3, 4 (radula).

Collisella (Notoacmea) petterdi. — Christiaens, 1975b: 103. (See Macpherson (1955) for full synonymy).

Diagnosis. *Shell* (pl. 3, figs 4-6). Elliptical, generally flattened, apex anterior, anterior and posterior slopes slightly convex. Concentric growth rings apparent in southern specimens, but usually lacking in northern ones, sculptured with widely-spaced, rounded, smooth radial riblets. Light brown in colour with numerous darker brown radiating bands, although bands often indistinct due to erosion. Interior pale to dark-brown; margin often with lighter bands, usually a white zone inside margin.

Radula (pl. 10, figs 1-2). Inner laterals very long and pointed with long bases. Outer lateral teeth with short bases; inner cusps approximately $\frac{1}{2}$ size of inner lateral teeth and less pointed; outer cusps approximately $\frac{2}{3}$ size of inner cusps and rounded. Radular segment longer than broad.

Dimensions

	Height	Length	Width
Holotype (from original description)	7mm	22mm	20mm
Large specimen (Sydney)	7.8	21.0	17.6
Large specimen (south Tasmania)	7.5	23.0	20.0
Large specimen (Victoria, figured)	8.75	22.1	19.55

Type. Holotype, TM, E343/7684; north west coast of Tasmania.

Distribution. Eastern South Australia, Tasmania, Victoria, New South Wales, to Noosa Heads in south Queensland. Found on vertical rock faces in the upper littoral.

Remarks. Juveniles of this species are sometimes confused with darkly-coloured specimens of *N. flammea*. They can, however, be readily separated by their different internal coloration and exterior sculpture. *N. petterdi* is brown internally, whereas *N. flammea*, although variable in colour, is never brown. Externally *N. flammea* is sculptured with fine, widely-spaced, granular riblets whereas *N. petterdi* has coarser, smooth, even more widely-spaced ribs.

There are also differences in habitat. *N. petterdi* is found almost exclusively on vertical rock faces in the upper littoral, whereas *N. flammea* occurs lower on the shore on a wide variety of surfaces.

This species is similar to the New Zealand type species of *Notoacmea*, *N. pileopsis* (Quoy & Gaimard) but differs in having a radial pattern of pale bands instead of a series of disconnected, irregular, oval, pale spots. The radial sculpture is heavier in the Australian species, consisting of widely-spaced, rounded ribs whereas in *N. pileopsis* the radial ribs are sharp, rather weak and closer together.

Genus *Collisella* Dall, 1871.

Type species (original designation): *Acmaea cassis* Eschscholtz, 1833 = *A. pelta* Eschscholtz, 1833.

Christiaens (1975b) has suggested the use of this genus for several Australian species. He also includes several other genus-group taxa, including *Notoacmea*, as subgenera of *Collisella* as discussed above.

Collisella mixta (Reeve, 1855). Pl. 4, figs 7-15, pl. 11, figs 1, 2.

Patella mixta Reeve, 1855: pl. 39, fig. 129.

Acmaea flammea. — Verco, 1906: 212; Verco, 1907: 101; Pritchard & Gatliff, 1903: 196 (in part, *non* Quoy & Gaimard, 1834).

Chiazacmea flammea conoidea. — Oliver, 1926: 560 (in part, *non* Quoy & Gaimard, 1834).

Chiazacmea flammea mixta. — Oliver, 1926: 560 (in part).

Notoacmea granulosa Macpherson, 1955: 252, fig. in text, pl. 17, figs, 3, 4 (radula).

Chiazacmea conoidea. — Cotton, 1959: 304, fig. 202 (in part, *non* Quoy & Gaimard, 1834).

Chiazacmea mixta. — Cotton, 1959: 306, fig. 203 (in part).

Chiazacmea flammea. — Cotton, 1959: 304, fig. 201 (? in part, *non* Quoy & Gaimard, 1834).

Collisella (*Collisella*) *granulosa*. — Christiaens, 1975b: 100.

Collisella (*Collisella*) *mixta*. — Christiaens, 1975b: 101.

Diagnosis. *Shell* (pl. 4, figs 7-15). Rather solid, often tall, with apex at about anterior $\frac{1}{3}$. Anterior slope straight; posterior slope convex. Surface with faint to strong irregular radial ribs (usually eroded), sometimes nearly smooth. Grey-brown to yellowish in colour with darker reticulate patterns or dark radial rays. A "Maltese Cross" pattern often evident. Interior with pale to dark-brown blotches on white, margin lined with dark brown.

Radula (pl. 11, figs 1, 2). All lateral teeth short and stout. Inner cusp of outer lateral teeth nearly as long as inner lateral teeth; rounded outer cusps about 2/3 length of inner lateral teeth and wedge-shaped. Marginal teeth very short and curved. Inner lateral teeth with long bases, outer lateral teeth with short bases. Radular segment longer than broad.

Dimensions

	Height	Length	Width
Lectotype of <i>P. mixta</i>	6.1mm	16.6mm	12.7mm
Paralectotype of <i>P. mixta</i>	6.67	17.50	14.04
Holotype of <i>N. granulosa</i>	7.64	14.46	10.20
Large specimen (Robe, South Australia)	7.9	21.3	10.9
Small, tall specimen (Port Fairy, Victoria)	6.1	10.0	7.1

Types. *P. mixta*. Lectotype (pl. 4, figs 7-9), BMNH (197825) and paralectotype (pl. 4, figs 10-12) (197826); Port Phillip Bay, Victoria, coll. H. Benson, ex Cuming colln. *N. granulosa*. Holotype (pl. 4, figs 13-15), N.M.V. (F. 16131), paratypes (F. 5834); locality not given in original description, Warrnambool, Victoria on label.

Distribution. Southern Australia from Robe in South Australia to Lakes Entrance in Victoria, and Tasmania (uncommon). Lives in the mid to upper littoral of exposed open platforms.

Remarks. Reeve's 2 syntypes include his figured specimen which is here chosen as the lectotype. Macpherson (1955), like most previous authors, regarded *Patella mixta* as a synonym of *Chiazacmea flammae* auct. (= *Patelloida insignis* (Menke) herein). Reeve's types are the species named *Notoacmea granulosa* by Macpherson (1955), although they are more weakly sculptured and the shells less elevated than the type specimen of *granulosa*. The paralectotype of *P. mixta* bears a well developed "Maltese Cross" but the convex postero-dorsal margin, the remnants of a tessellate colour pattern and the weak, granulose sculpture show it also to be the species previously called *granulosa* rather than the superficially similar *P. insignis*.

Cotton's (1959) interpretation of *Chiazacmea mixta* is apparently a compound of *P. insignis* (Menke) and *C. mixta*.

Macpherson gives the height of the holotype of *N. granulosa* as 13mm but it is actually much less than this (7.64mm). A few specimens do, however, develop tall shells and closely resemble *Notoacmea alta* in outline. The flecked, irregular colour pattern of white, yellow and dark brown, the streaks of brown on the spatula and the presence of weak, simple ribbing externally are usually useful recognition characters of such specimens of *C. mixta*. The closely related *C. onychitis* does not seem to develop these high-spined forms.

A few specimens from South Australia (Streaky Bay and Coffin Bay) have almost smooth shells and a moderately elevated profile but the apex is anteriorly placed and the long posterior "slope" rather conspicuously convex. The colour pattern is sometimes tessellate and the specimens resemble, in general appearance, *Notoacmea flammae*, although they differ in sculpture and in the markedly convex posterior slope. Their radulae are the same as those of *C. mixta* and *C. onychitis* and because the shells of these specimens are closest to *C. mixta* they are tentatively included with that species.

Collisella onychitis (Menke, 1843). Pl. 4, figs 1-6, pl. 10, figs 5-7.

Patella onychitis Menke, 1843: 34; Hedley, 1923 : 309.

Acmaea (*Notoacmaea*) (sic!) *achates*. — Thiele, 1930: 564 (? non Reeve, 1855, pl. 38, fig. 123a, b).

Notoacmea onychitis. — Macpherson, 1955: 251, figs in text, pl. 17, figs 1, 2 (radula).

Collisella (*Collisella*) *onychitis*. — Christiaens, 1975b: 101.

Diagnosis. Shell (pl. 4, figs 1-6). Ovate, thick, sculptured with approximately twenty weak to strong, rounded, radiating ribs, which are closer together at the anterior end. Margin thin and crenulated. Shell often eroded. Ribs cream in colour, often with elongated,

brown markings. Interspaces between ribs dark brown, often flecked with white. Interior procellaneous and usually whitish; margin showing exterior pattern.

Radula (pl. 10, figs 5-7). As in *C. mixta*.

Dimensions

	Height	Length	Width
Dimensions given in original description (converted to mm using 1 linie = 2.18mm)	6.5mm	24.0mm	20.5mm
Large specimen (Albany)	9.7	22.4	19.6

Type. *P. onychitis*. Type lost; Western coast (of Australia).

Distribution. Western Australia southwards from Quobba, to Ceduna in western South Australia. On rocks in the lower littoral.

Remarks. This species is related to *C. mixta* which is very common in Victoria but rare in Tasmania and most of South Australia whereas *C. onychitis* is abundant in south Western Australia. Thus there is an apparent separation in the distribution of the two species. The radulae of *C. onychitis* and *C. mixta* are almost identical but they are generally very easily separated on shell characters. *C. onychitis* is a variable species in shape, colour and sculpture of the shell. Two sculptural forms are figured (pl. 4, figs 1-6).

Menke's name and rather brief description almost certainly refers to a specimen of the species described above with which it was first associated by Macpherson (1955). The loss however of most of Menke's type material, including the type of *P. onychitis*, makes this opinion impossible to confirm.

Genus *Patelloida* Quoy & Gaimard, 1834.

Type species (subsequent designation, Gray, 1847): *P. rugosa* Quoy & Gaimard, 1834.

Synonyms: *Collisellina* Dall, 1871. Type species (original designation): *Patella saccharina* Linne', 1758. *Chiazacmea* Oliver, 1926. Type species (original designation): *Patelloida flammea* auct. = *Acmaea crucis* T. Woods, 1876.

Remarks. Oliver (1926) recognised two subgenera of *Patelloida*, *Patelloida* ss. and *Collisellina* Dall, 1871. These were separated on rather minor shell characters and are not upheld by Moskalev (1966). *Chiazacmea* Oliver, which was given full generic rank by Oliver (1926) and Macpherson (1955), is also reduced to a synonym of *Patelloida* by Moskalev (1966). We can find no good reasons why any of these names should be re-employed.

Unfortunately none of the species previously placed in *Chiazacmea* was examined by MacClintock (1967) so that their shell structure is not known. Moskalev (1966) regards *Chiazacmea* as a synonym of *Patelloida* on the basis of the similarity of the radular features. The Australian species included in *Chiazacmea* by Oliver (1926) and Macpherson (1955) form a group somewhat distinct from "typical" *Patelloida* species in shell characters, as they tend to be rather small with weak or obsolete ribbing. *Chiazacmea heteromorpha* Oliver approaches more typical species of *Patelloida* in size and sculpture, having moderate ribbing, a thick shell and, occasionally, a spotted spatula as in species formerly placed in *Collisellina*. *Acmaea mufria* Hedley, although usually rather small, often has distinct ribbing but has been placed in *Chiazacmea*, being closely related to the type species. Because there is no clear-cut distinction in shell features and because the radular characters of species included in *Chiazacmea* are identical to those in *Patelloida*, *Chiazacmea* is regarded as a synonym of *Patelloida*.

Oliver designated as the type species of his genus *Chiazacmea* "*Patelloida flammea* Q & G. (Hobart) (as herein defined)". There is no doubt that Oliver intended as the type species the species here shown to be *Patelloida insignis* (Menke). The type specimen(s) of *insignis* were taken in Western Australia and Oliver regarded Tasmanian material as typical of his

flammea. Consequently the earliest name for the Tasmanian form of *P. insignis* is taken as the type of the genus but a submission will have to be made to the ICZN to formalise this matter.

Patelloida alticostata (Angas, 1865). Pl. 5, figs 1-6.

Patella alticostata Angas, 1865: 56.

Patella costata. — auct. (non Sowerby, 1839).

Patelloida alticostata antelia Iredale, 1924: 234.

Patelloida alticostata complanata Iredale, 1924: 234.

Patelloida alticostata. — Macpherson, 1955: 240, pl. 11, figs 1, 2 (radula); Christiaens, 1975b: 94.

(See Oliver (1926 : 551) and Macpherson (1955 : 240) for full synonymy).

Diagnosis. *Shell* (pl. 5, figs 1-6). Large, conical, thick and heavy. Apex slightly anterior and usually eroded. Margin thin and scalloped. Surface sculptured with approximately 18 strong, rounded, radiating ribs, which are often closer together at the anterior end. White or grey in colour with darker ribs; interspaces between ribs marked with characteristic fine, black cross lines. Interior porcellaneous and mostly white; margin black, or with black and white spots; remainder of interior white, often with black blotches on the spatula.

Radula. Inner lateral teeth with long, broad cusps and long bases. Outer lateral teeth with very broad and rounded inner cusps; outer cusps approximately $\frac{1}{4}$ size of inner cusps and more pointed. Marginal teeth large and spoon-shaped. Radular segment square.

Dimensions

	Height	Length	Width
Holotype	11.9mm	36.0mm	29.6mm
Large specimen (Albany, Western Australia)	19.1	52.8	48.0

Types. *P. alticostata*. Holotype, BMNH, 1870.10.26.163; Port Lincoln, South Australia. *P. alticostata antelia*. Not found. Peronian Province (localities mentioned are Sydney Harbour and Twofold Bay, New South Wales; Lakes Entrance and Melbourne Heads, Victoria). *P. alticostata complanata*. Not found. Sydney, New South Wales, below low water.

Distribution. Occurs from Geraldton in Western Australia, around the southern part of Australia (including Tasmania) to the mid-north coast of New South Wales. Lives on exposed rocks in the lower littoral and shallow sublittoral.

Remarks. Macpherson (1955) discusses the variation in this species which Oliver (1926) treats as two subspecies. This is one of the commonest of the temperate Australian limpets and it exhibits considerable variation, particularly in the strength of the ribbing. Some shells are virtually smooth; others strongly ribbed (cf. pl. 5, figs 2 and 5) but every gradation occurs between these extremes.

The name *costata* Sowerby, 1829 has been used by various authors for *P. alticostata*, most recently by Dance (1974 : 36). Christiaens (1975b : 94) also indicates that they are the same. Tomlin (1924 : 98) has discussed the matter at length and concluded, without doubt, that the type of *Lottia* (?) *costata* Sowerby was *Patella longicosta* Lamarck from South Africa. The holotype (pl. 8, figs 13-15), in the BMNH (1912.2.22.5), is certainly very similar to *P. longicosta* but differs from all of the material available to us of that species in having several small, dark, blotches on the spatula. It does not exactly match any other species in *Patella* (*Patellanax*), where it appears to belong, and so we somewhat tentatively concur with Tomlin's opinion.

Patelloida bellatula (Iredale, 1929). Pl. 5, figs 7-9, pl. 11, fig. 4.

Collisellina bellatula Iredale, 1929: 275, pl. 31, fig. 13.

Diagnosis. *Shell* (pl. 5, figs 7-9). Small, thick, low, apex slightly anterior. Sculpture of irregular, prominent, rounded radial ribs over which run fine radial riblets; interspaces between riblets dark-brown (appear as narrow, brown, radial lines). Remainder of shell white on both exterior and interior surfaces except spatula which is often blotched with pale brown.

Radula (pl. 11, fig. 4). Inner lateral teeth with large, broad cusps. Outer lateral teeth large, with only slightly rounded cusps; outer cusps of approximately same size as inner ones. Both lateral teeth with short bases. Marginal teeth long with very broad, spoon-shaped cusps. Radular segment much broader than long.

Dimensions

	Height	Length	Width
Large paratypes	6.46mm	16.10mm	11.21mm
	4.30	15.36	12.06

Types. Holotype not located. Many paratypes (pl. 5, figs 7-9), AMS, C.53558; Michaelmas Cay, off Cairns, Queensland.

Distribution. Tropical Queensland, on the Barrier Reef Islands north from Palm Islands (off Townsville) to New Guinea. On beach rock, coral and dead shells, usually subtidal.

Remarks. This species was overlooked by Macpherson (1955). It is more elongate and has a paler interior and much more pronounced ribs than *P. rugosa* Quoy & Gaimard. It lives (at Lizard Island, north Queensland) on *Lithothamnion* covered coral and on large shells from the lower littoral to several metres deep. It produces a very pronounced home 'scar' on the substratum and is often covered with *Lithothamnion*.

Christiaens (1975a) erroneously included this species in the synonymy of *P. saccharina* (Linné).

Patelloidea cryptalirata (Macpherson, 1955). Pl. 5, figs 10-15, pl. 10, figs 3, 4.

?*Acmaea septiformis*. — T. Woods, 1880: 111 (*non* Quoy & Gaimard, 1834).

Chiazacmea cryptalirata Macpherson, 1955: 250, figures in text, pl. 16, figs 1, 2 (radula).

Chiazacmea ater Macpherson, 1955: 250, figures in text, pl. 16, figs 3, 4 (radula).

Patelloidea cryptalirata. — Christiaens, 1975b : 94.

Diagnosis. *Shell* (pl. 5, figs 10-15). Thin, ovate and flattened. Apex at about anterior third. Slopes straight or slightly convex. Surface almost smooth. Cream or light brown in colour, overlain with a red-brown, fine reticulate pattern and fine radial lines; sometimes a few broad, dark-brown to black radial bands. Occasional specimens with irregular "Maltese Cross" pattern. Interior with bluish rim around muscle scar; spatula usually brown, margin showing external colour pattern.

Radula (pl. 10, figs 3, 4). Inner lateral teeth with pointed cusps and short bases. Outer lateral teeth with short bases; inner cusps broad, pointed, about equal in length to cusps of inner lateral teeth; outer cusps small, rounded. Marginal teeth long, with curled cusps. Radular segment wider than long.

Dimensions

	Height	Length	Width
<i>C. cryptalirata</i> (from original description)	4mm	12mm	9.5mm
Actual dimensions of specimen labelled as holotype	3.4	10.3	8.9
Dimensions of actual holotype	3.76	12.10	9.25
	Height	Length	Width
<i>C. ater</i> (from original description)	3.5	11	8.5
Actual dimensions of holotype	2.75	11.00	8.70

Types. *C. cryptalirata*. Holotype NMV, F. 13861 (part), 1 paratype F. 13861 (part); on sheltered rock faces in littoral zone, Point Vernon, "Yeppoon" (= Hevey Bay) Queensland. Paratype (specimen labelled as holotype) Wreck Point, Yeppoon, Queensland (NMV, F.13856) (pl. 5, figs 10-12). *C. ater*. Holotype (pl. 5, figs 13-15), NMV, F.13974, and 1 paratype; on the under-surface of rocks in mid-littoral, Bargara, Queensland.

Distribution. Northern Australia from Hervey Bay in southern Queensland to Broome in north Western Australia and Papua New Guinea. Found in sheltered habitats (e.g. crevices, undersides of boulders) throughout the intertidal zone.

Remarks. Examination of a large range of material from Queensland indicates that Macpherson's two species are extremes of one somewhat variable species. This conclusion was also reached by B.J. Smith in Christiaens (1975b).

The holotype of *C. cryptalirata* so labelled in the NMV shows a different locality (Wreck Point, Yeppoon) from that given by Macpherson but the registered number is the same (misprinted as F.1385b on the label). It is certain that the specimen labelled as such is not the holotype, particularly when the dimensions given by Macpherson differ so widely from those of this specimen. One of the two paratypes from Point Vernon (F.13861) agrees closely with the published dimensions of the holotype of *Cryptalirata* and the locality also coincides. This specimen is here assumed to be the holotype. Macpherson's figure, however, does not agree closely with any of the type specimens.

Patelloida heteromorpha (Oliver, 1926). Pl. 5, figs 16-18, pl. 12, figs 1-3.

Chiazacmea heteromorpha Oliver, 1926: 562, pl. 99, fig. 1, text fig. C; Macpherson, 1955: 249, fig. in text, pl. 15, figs 3, 4 (radula).

Diagnosis. *Shell* (pl. 5, figs 16-18). Small, thick, rough (but usually without definite ribbing) and often eroded. Apex slightly anterior; slopes straight to lightly convex; margin often irregular. Sculptured with fine radial striae and a few very weak radial ribs sometimes evident. Pale brown to whitish in colour, with several, very dark, irregular, radial bands, which may coalesce and are often not clearly evident on the exterior. Juvenile shells with a dark-brown zig-zag pattern on white. Spatula pale-bluish to dark-brown, sometimes showing a pattern of small dark spots; margin white to pale-brown with black stripes, or completely black.

Radula (pl. 12, figs 1-3). Inner lateral teeth with pointed cusps and with moderately long bases. Outer lateral teeth have short bases; inner cusps very broad and only slightly rounded (often square); outer cusps very small and rounded. Marginal teeth long and curl in behind inner laterals. Radular segment longer than broad.

Dimensions

	Height	Length	Width
Holotype	8.00mm	18.05mm	15.93mm
Large specimen (Cooktown)	5.9	18.6	14.5

Types. Holotype (pl. 5, figs 16-18), AMS, C.105728. Facing Island, Port Curtis, Gladstone, Queensland. Living on rocks between tide marks in the *Ostrea* (= *Saccostrea*) *cucullata* (Born) association and above.

Distribution. Queensland, from Hervey Bay in the south to Cooktown in the north. Lives in mid to high littoral habitats usually on sloping surfaces in sheltered, usually silty locations.

Remarks. This species is sympatric with *P. cryptalirata* (Macpherson) over all of its range but can be readily distinguished by its larger, heavier shell, darker interior, more centrally placed apex, external radial sculpture and, when non-eroded, characteristic pattern of white zig-zag lines on the juvenile shell. The spotted spatula is seen in some specimens and is a feature shared by *P. latistrigata* (Angas) and *P. saccharina*. The zig-zag colour pattern on the juvenile shell is similar to the colour pattern of *P. saccharina* but that species attains a

much larger size, has a pale interior and often has a star-shaped outline due to the presence of very strong external ribs. *P. heteromorpha* has very weak ribs which only slightly crenulate the margin of the shell.

Christiaens (1975b) suggests that *P. heteromorpha* may be a subspecies of *P. latistrigata* on the basis of intermediate specimens from Yeppoon and a similar radula. This observation is not upheld because of the considerable sculptural, textural and colour differences between the shells of the two species. The radulae are very similar but *P. heteromorpha* differs from *P. latistrigata* in the inner lateral teeth having relatively shorter bases. We have not seen any "intermediate" specimens despite the examination of large series from Yeppoon and other areas.

Patelloida insignis (Menke, 1843). Pl. 6, figs 1-6, pl. 12, figs 4-6.

Patella insignis — Menke, 1843: 34.

Acmaea crucis — T. Woods, 1876: 52; T. Woods, 1877: 44; Thiele, 1930: 564.

Acmaea cruciata. — Tate & May, 1901: 411 (non Linné, 1758).

Acmaea flammea. — Verco, 1906: 212, Verco, 1907: 101; Pritchard & Gatliff, 1903: 196 (in part, non Quoy & Gaimard, 1834).

Radiacmaea insignis. — Iredale, 1924: 235.

Chiazacmaea flammea flammea. — Oliver, 1926: 558; Macpherson, 1955: 247, fig. in text, pl. 14, figs 1, 2 (radula) (non Quoy & Gaimard, 1834).

Chiazacmaea flammea conoidea. — Oliver, 1926: 560 (in part, non Quoy & Gaimard, 1834).

Chiazacmaea flammea mixta. — Oliver, 1926: 560 (in part), fig. B.

Chiazacmaea mixta. — Cotton, 1959: 306, fig. 203 (in part, non Reeve, 1855).

Chiazacmaea flammea. — Macpherson & Gabriel, 1962: 50, fig. 66 (non Quoy & Gaimard, 1834).

Patelloida (*Patelloida*) *flammea*. — Christiaens, 1975a: 76 (non Quoy & Gaimard, 1834).

Collisella (*Collisella*?) *crucis*. — Christiaens, 1975b: 96.

Patelloida conoidea insignis. — Christiaens, 1975b: 96.

Diagnosis. Shell (pl. 6, figs 1-6). Of moderate size (generally larger than in *P. mufria* (Hedley)) thick, ovate, sometimes flattened, usually moderately elevated, sometimes high-spined. Apex slightly anterior; slopes straight or with posterior slope slightly convex. Sculptured with numerous fine, simple, radial striae or weak riblets, often becoming obsolete in large specimens, striae usually equal to, or narrower than, the interspaces. White or greyish in colour, with irregular blotches and radial markings of dark brown, often concentrated into a "Maltese Cross". Interior porcellaneous, white and brown, often showing exterior pattern.

Radula (pl. 12, figs 4-6). Inner lateral teeth with rounded cusps and medium-sized bases. Outer lateral teeth with short bases; inner cusps broad and only slightly rounded, almost as long as cusps on inner lateral teeth; outer cusps rounded, about 1/3 size of inner cusps. Marginal teeth long and spoon-shaped. Radular segment broader than long.

Dimensions.

	Height	Length	Width
<i>A. crucis</i> (from original description)	19mm	31mm	31mm
Lectotype of <i>A. crucis</i>	17.45	31.10	25.00
Paralectotype of <i>A. crucis</i> (AMS)	9.90	21.75	16.35
Largest paralectotype of <i>A. crucis</i> (TM)	—	39	—
Large Western Australian specimens (Augusta)	6.66	20.55	14.70
	8.25	20.20	15.30

Types. *P. insignis*. Lost. *A. crucis*. Lectotype (pl. 6, figs 4-6) (here chosen) AMS, C.105257, and paralectotype C.105257, 3 paralectotypes, TM, E304/7681.

Distribution. Southern and western Australia from Geraldton in Western Australia to

South Australia and in Tasmania. Found subtidally and in the lower littoral regions of sheltered coasts.

Remarks. The type of *Patella insignis* has been lost but Menke's description and his subsequent note on the species (Menke, 1844) leave little doubt as to its identity. Iredale (1924) noted the relationship of *crucis* T. Woods to *insignis*, regarding the latter to be the "Western Australian representative of *crucis*".

This species has had an extremely complex nomenclatural history as briefly outlined in the synonymy, much of the confusion being brought about by a failure of almost every author other than Iredale (1924) to recognise the real identity of *Patelloida flammea* Quoy & Gaimard.

Hedley (1915) states that Iredale informed him that the types of *Acmaea inradiata* Reeve, 1855 were identical with *Acmaea crucis*. Reeve gave no habitat but the type tablet in the BMNH was (later?) marked "Tasmania". Later Iredale (1924) noted that, on closer examination, none of the reputed 3 "types" was the specimen figured by Reeve and he advocates the rejection of *inradiata* from the Australian fauna.

Tate & May (1901) place *flammea* and *crucis* in synonymy with *A. cruciata* (Linné, 1758), a species from the tropical Pacific. This interpretation is correctly rejected by Verco (1906).

The type material of *Patella gealei* Angas, 1865 consists of two corroded "types" one of which, as determined by Iredale (1924 : 237), is *Acmaea "crucis"* (i.e. *P. insignis*) and the other "a *Patella*" (= *Cellana tramoserica* (Holten)). It is the latter species which must be regarded as the type because, as pointed out by Iredale, it was the only specimen in Angas's possession when the species was described.

Patelloida mufria (Hedley) has an almost identical shell but the radula of that species has much broader outer cusps on the outer lateral teeth than does *P. insignis*. The shell of *P. mufria* does not attain the size of *P. insignis*. The two species are contrasted in more detail below (under *P. mufria*).

Adam & LeLoup (1938) record *Acmaea crucis* T. Woods from New Caledonia but Christiaens (1975b) has renamed their specimens *Collisella (Notoacmea) adami*.

Patelloida latistrigata (Angas, 1865). Pl. 7, figs 1-4, pl. 10, figs 8, 9.

Patella latistrigata Angas, 1865 : 154.

Acmaea marmorata T. Woods, 1876 : 156; Henn & Brazier, 1894 : 178; Tate and May, 1901 : 412; Verco, 1906 : 210; Torr, 1914 : 366, pl. 20, fig. 8a, b (radula).

Acmaea marmorata var. *submarmorata* Pilsbry, 1891 : 52, pl. 42, figs 69, 70.

Acmaea gaelie. — Pritchard & Gatliff, 1903 : 198 (non Angas, 1865).

Patelloida submarmorata. — Iredale, 1924 : 236; Thornley, 1945 : 26, figs 3a, b.

Patelloida (Collisellina) latistrigata latistrigata. — Oliver, 1926 : 556.

Patelloida (Collisellina) latistrigata submarmorata. — Oliver, 1926 : 558.

Patelloida latistrigata latistrigata. — Macpherson, 1955 : 245, fig. in text, pl. 13, figs 1, 2 (radula).

Patelloida latistrigata submarmorata. — Macpherson, 1955 : 245, fig. in text, pl. 13, figs 3, 4 (radula).

Collisellina latistrigata. — Cotton, 1959 : 302, fig. 200.

Collisellina marmorata. — Cotton, 1959 : 303.

Collisellina gealei. — Cotton, 1959 : 303 (non Angas, 1865).

Patelloida (Patelloida) latistrigata. — Christiaens, 1975a : 76.

Diagnosis. Shell (pl. 7, figs 1-4). Small, elevated, often pitted and worn. Variable number of irregular rounded ribs, usually more in northern populations than in southern ones. Light greyish-brown in colour where surface eroded, otherwise dark-brown. Interior porcellaneous, grey/brown, with spatula characteristically spotted with blue or brown and often bordered with white. Spotted pattern usually evident on exterior of eroded specimens. Internal marginal area white or yellowish with black or brown stripes or irregular markings; edge usually dark.

Radula (pl. 10, figs 8, 9). Inner lateral teeth with narrow and pointed cusps and with very long bases. Outer lateral teeth stout, with short bases; inner cusps broad and rounded, much larger than outer cusps. Marginal teeth very long and curled in behind inner lateral teeth. Radular segment much longer than broad.

Dimensions.

	Height	Length	Width
Holotype of <i>P. latistrigata</i>	6.0mm	17.8mm	11.7mm
Type of <i>A. marmorata</i> (from original description)	6	21	15
Lectotype of <i>A. marmorata</i> var <i>submarmorata</i>	6.30	16.15	13.40
Paralectotype	6.2	15.9	12.9
Large specimen (Lakes Entrance, Victoria)	7.6	23.4	17.5

Types. *P. latistrigata*. Holotype (pl. 7, figs 1, 2), BMNH, 70.10.26.159; Aldinga Bay, South Australia. *A. marmorata*. 2 probable syntypes, TM, 5595, E336/7677; Tasmania. *A. marmorata* var. *submarmorata*. Lectotype (here chosen) (pl. 7, figs 3, 4) and paralectotype, ANSP, 50046; Port Jackson, New South Wales.

Distribution. Occurs in eastern South Australia, Tasmania, Victoria, New South Wales and southern-most Queensland. Lives on exposed rock surfaces in the mid and upper littoral, usually in association with the barnacle *Tesseropora rosea* (Krauss).

Remarks. The eastern Australian form of *P. latistrigata*, named *submarmorata* by Pilsbry, is smaller, with generally weaker, more even ribbing than the southern form. Iredale (1924) and Cotton (1959) regard *latistrigata* and *submarmorata* as separate species. Oliver (1926) considered them to be subspecies, an interpretation which we see as unnecessary because of the large numbers of intermediate specimens encountered, particularly in the Bass Strait area.

Cotton (1959) used the name *marmorata* T. Woods for the southern Tasmanian form of *P. latistrigata* which he separates as a distinct species. The same author used *gealei* Pritchard & Gatliff, 1903 (*non* Angas) for the Victorian "species". These interpretations appear to be completely unjustified, Victorian, South Australian and Tasmanian shells all being virtually identical and showing no radular differences.

A shell in the AMS identified as the holotype of *A. marmorata* (C. 5202) and said to come from Manly, New South Wales, is a specimen of *P. saccharina stella* (Lesson). This specimen has no type status as it disagrees with the original description, dimensions and locality. The 2 "syntypes" in the Tasmanian Museum are also questionably types as Hardy (1915 : 67) states that there is no documentation with the specimens to indicate that they are authentic.

Macpherson (1955) records this species from Queensland but specimens in the NMV identified as *P. latistrigata submarmorata* from Elliot River Head, Bargara and Yeppoon are *P. heteromorpha*. No specimens of *P. latistrigata* north of Coolangatta, southern-most Queensland, are known to the authors.

Patelloida mimula (Iredale, 1924). Pl. 6, figs 7-16, pl. 11, figs 5-8.

Patella jacksoniensis Reeve, 1855: pl. 39, fig. 127 (*non Patella jacksoniensis* Lesson, 1830).

Acmaea mixta. — Hedley, 1915: 713 (in part, *non* Reeve, 1855).

Notoacmaea mixta mimula Iredale, 1924: 235 (*nom. nov. pro Patella jacksoniensis* Reeve, 1855, *non* Lesson, 1830); Thornley, 1945: 26, figs 4a, 4b.

- *Chiazacmaea flammea queenslandiae* Oliver, 1926: 561; Macpherson, 1955: 247, fig. in text, pl. 14, figs 3, 4 (radula).

Chiazacmaea (sic.) *flammea*. — Anderson, 1965: 109, figs 9-13 (*non* Quoy & Gaimard, 1834).

- *Patelloida flammea marrowi* Christiaens, 1975a: 76, pl. 2, fig. 7; Christiaens, 1975b: 95.
- Patelloida flammea mimula*. — Christiaens, 1975b: 95.

Diagnosis. Shell (pl. 6, figs 7-16). Small, thin smooth and conical. Apex only slightly anterior. Slopes straight. Brown or greenish in colour, with irregular dark-brown radial marks often forming a "Maltese Cross" pattern. Interior light brown or cream, and showing exterior pattern especially at the margin.

Radula (pl. 11, figs 5-8). Inner lateral teeth have short bases; cusps stout, relatively short and pointed. Outer lateral teeth have short bases; inner cusps rounded; outer cusps very small, closely abutting on to inner cusps but slightly more rounded. Marginal teeth long with large spoon-shaped cusps. Radular segment broader than long.

Dimensions

	Height	Length	Width
Lectotype of <i>P. jacksoniensis</i> Reeve	7.3mm	19.5mm	14.3mm
Paralectotypes of <i>P. jacksoniensis</i>	6.9	19.6	13.4
	6.20	18.85	14.15
	5.35	15.10	11.55
Holotype of <i>C. flammea queenslandiae</i>	5.40	13.73	10.01
Holotype of <i>P. flammea marrowi</i>	4.7	9.5	7.6
Large specimen (Sydney)	7.50	19.05	14.65

Types. *N. mixta mimula* nom. nov. pro *P. jacksoniensis* Reeve. Lectotype (pl. 6, figs 7, 8) (here chosen) BMNH, 197829 and 3 paralectotypes (pl. 6, figs 9, 10), BMNH, 197830; New South Wales. *C. flammea queenslandiae*. Holotype (pl. 6, figs 11-13), AMS, C.105729; Port Curtis, Gladstone, Queensland, living on rocks between tides in the *Ostrea* (= *Saccostrea*) *cuculata* association. *P. flammea marrowi*. Holotype (pl. 6, figs 14-16), NMV, F29550. Paratypes in NHMP. Wallal Downs, Eighty Mile Beach, north Western Australia.

Distribution. From Lakes Entrance in eastern Victoria, through New South Wales and Queensland, the Northern Territory and north Western Australia. Lives in sheltered habitats in estuaries, usually in association with the oyster *Saccostrea*.

Remarks. Iredale's name was introduced as a replacement for *Patella jacksoniensis* Reeve non Lesson, a fact overlooked by Macpherson (1955) who includes *P. jacksoniensis* in the synonymy of *Chiazacmea flammea queenslandiae*. Macpherson's *Chiazacmea flammea mimula* is, at least in part, *Patelloida mufria*.

This species extends continuously along the entire east, north and north-western coasts of Australia. It has been given a separate name in north Western Australia (*marrowi* Christiaens) but the differences exhibited by northern and northwestern specimens (mainly smaller size) appear to be clinal. There are no significant differences in the radulae of tropical and temperate populations nor between those on the northern, north-western and south-eastern coasts.

The radula of this species is similar to that of *P. insignis* in most respects but differs in having relatively larger marginal teeth. The colour of the foot is a useful means of distinguishing *P. mimula* and *P. mufria*, which are sympatric in New South Wales, *P. mimula* having an orange foot and *P. mufria* a grey foot.

Patelloida mufria (Hedley, 1915). Pl. 7, figs 5-13, pl. 13, figs 1-4.

Acmaea subundulata. — Whitelegge, 1889: 272 (in part ?, non Angas, 1865).

Acmaea inradiata. — Hedley, 1915: 712 (non Reeve, 1855).

Acmaea mufria Hedley, 1915: 713, pl. 81, figs 50-52.

Radiacmea insignis cavilla Iredale, 1924: 235; Thornley, 1945: 27, figs 12 a-d.

Radiacmea mufria. — Iredale, 1924: 235. Thornley, 1945: 27, figs 11a-d.

Chiazacmea mufria. — Oliver, 1926: 562.

Chiazacmea flammea cavilla. — Oliver, 1926: 561.

Notoacmea (unnamed) Thornley, 1945: 27, figs 8a-b.

Chiazacmea flammea mimula. — Macpherson, 1955: 248, figure in text, pl. 15, figs 1, 2 (radula) (in part, non Iredale, 1924).

Patelloida (*Patelloida*) *mufria*. — Christiaens, 1975a: 76.

Patelloida cavilla. — Christiaens, 1975b: 96.

Diagnosis. Shell (pl. 7, figs 5-13). Small, usually thin, ovate, generally moderately elevated (but specimens may be very elevated or very flattened depending on the environment). Sculptured with numerous fine to rather strong, smooth radial lirae, usually wider than the spaces between. Apex slightly anterior. Anterior slope straight, posterior slope straight or convex. Whitish in colour, overlain with a variable pattern of dark brown flecks and radial markings often in the form of a "Maltese Cross". Interior porcellaneous, and often showing exterior pattern.

Radula (pl. 13, figs 1-4). Inner lateral teeth with medium-sized, pointed cusps and rather short bases. Outer lateral teeth with short bases; inner cusps narrow, rounded and about 2/3 size of cusps of inner lateral teeth; outer cusps very broad and nearly as long as inner ones, rounded with a characteristic sloping or slightly convex edge on outer side. Marginal teeth long with small spoon-shaped cusps. Radular segment approximately square.

Dimensions

	Height	Length	Width
Lectotype of <i>A. mufria</i>	2.80mm	5.54mm	3.37mm
Large specimen (Sydney)	4.90	11.75	8.70

Types. *A. mufria*. Lectotype (pl. 7, figs 5-7), AMS, C.112908, and many paralectotypes AMS, C32440, C22531; Balmoral Beach, Middle Harbour, Sydney, New South Wales (lectotype and paralectotypes, (C.32440); Wreck Bay, New South Wales (paralectotypes, C.22531). *P. insignis cavilla*. Types not found; Sydney, New South Wales.

Distribution. Ballina in New South Wales south to Victoria and occasional records from South Australia and south Western Australia. Found subtidally or intertidally in sheltered to moderately exposed habitats, often on the shells of other gastropods.

Remarks. This species is extremely difficult to satisfactorily distinguish from *P. insignis* on shell characters, although the radulae of the two species are fairly distinct, especially in the relative width of the outer cusps of the outer lateral teeth. Both species are sympatric on the south coast (south Western Australia, South Australia and possibly Victoria), but *P. mufria* is apparently uncommon everywhere except New South Wales. The shell of *P. mufria* can be distinguished from adult *P. insignis* by its smaller size, usually coarser radial sculpture and fewer radial, dark-colour markings. We have, however, not been able to confidently distinguish small specimens of *P. mufria* and *P. insignis* on shell characters, their identity having to be confirmed by an examination of the radula.

The shell is variable, some specimens, like the lectotype, being minute, narrow and often tall, and are found living compressed between the ribs of *Thais orbita* (Gmelin) or amongst *Galeolaria* tubes. The larger, flatter specimens are found on smooth surfaces and, no doubt, conform to Iredale's *R. insignis cavilla*. Intermediate shapes are common and the radulae of the two forms are identical.

Further field work is required to more clearly delineate the ranges of both *insignis* and *mufria* and their ecological requirements in areas where they are sympatric.

Macpherson (1955) called this species *Chiazacmea flammea mimula*. Most of the material in the NMV identified by her is *P. mufria* but two lots are *P. mimula* (F.8403, F.14451).

Patelloida nigrosulcata (Reeve, 1855). Pl. 7, figs 14-16, pl. 12, figs 7, 8.

Patella nigrosulcata Reeve, 1855: pl. 30, fig. 84.

Acmaea patellavecta Verco, 1912: 195, pl. 15, figs 5-7.

Patelloida nigrosulcata. — Oliver, 1926: 550; Macpherson, 1955: 241, fig. in text, pl. 11, figs 3, 4 (radula).

Patelloida (Patelloida) nigrosulcata. — Christiaens, 1975a: 76.

Diagnosis. Shell (pl. 7, figs 14-16). Ovate, thick and moderately to slightly elevated, of moderate size. Numerous flat, rather narrow, radial ribs with very narrow interspaces

causing margin to be minutely scalloped. White or cream, often tinged with light brown especially between ribs. Interior creamy white, porcellaneous, sometimes with a few brown blotches.

Radula (pl. 12, figs 7, 8). Lateral teeth stout with short bases. Inner lateral teeth, broad, with short, pointed cusps. Inner cusps of outer lateral teeth small and rounded; outer cusps large, very broad, with straight cutting edges. Marginal teeth long with large, spoon-shaped cusps. Radular segment much broader than long.

Dimensions

	Height	Length	Width
Holotype of <i>A. patellavecta</i> (from original description)	14mm	31.5mm	23mm
Lectotype of <i>P. nigrosulcata</i>	8.9	28.6	20.7
Paralectotypes of <i>P. nigrosulcata</i>	21.6	39.0	31.0
	15.40	29.15	24.90
Large specimen (Recherche Bay, south Western Australia)	15.4	37.1	29.5

Types. *P. nigrosulcata*. Lectotype (pl. 7, fig. 16) (here chosen), BMNH, 197828, and 2 paralectotypes (pl. 7, figs 14, 15) BMNH, 197829; described from unknown habitat. *A. patellavecta*. Holotype, SAM, D13373; Cape Naturaliste, south Western Australia.

Distribution. South and mid Western Australia from Geraldton to Esperance. Generally found attached to the shells of other gastropods notably *Patella* (*Patellanax*) *laticostata* Blainville, which occurs in the lower littoral and subtidally.

Remarks. Macpherson (1955) records this species from western South Australia but Cotton (1959) does not. The only lot that could be located in the NMV from South Australia is from Robe in eastern South Australia and is almost certainly mislocalised.

This species has a very wide outer cusp on each outer lateral tooth and is very similar to *P. mufria* in this respect, although it differs considerably in shell characters, particularly in its much larger size.

Patelloida profunda calamus (Crosse & Fischer, 1864). Pl. 8, figs 1-5, pl. 13, figs 5-7.

Patella calamus Crosse & Fischer, 1864: 348; Crosse & Fischer, 1865: 42, pl. 3, figs 7, 8.

Acmaea calamus. — Verco, 1906: 211.

Acmaea calamus polyactina Verco, 1912: 199.

Patelloida calamus. — Hedley, 1916: 184.

Radiacmea calamus. — Iredale, 1924: 235.

Actinoleuca calamus. — Oliver, 1926: 567; Thornley, 1945: 27; Cotton, 1959: 314, fig. 211;

Macpherson & Gabriel, 1962: 51, fig. 68.

Actinoleuca polyactina. — Cotton, 1959: 315, fig. 212.

Patelloida (*Patelloida*) *calamus*. — Christiaens, 1975a: 76.

Collisella (*Parvacmea*) *polyactina*. — Christiaens, 1975b: 105.

Diagnosis. *Shell* (pl. 8, figs 1-5). Small to moderate in size, rather thin, ovate and elevated. Apex slightly anterior, slopes straight. Sculptured with numerous fine, unequal, radiating ribs. Dull white or yellow in colour with irregular brown to purplish markings. Interior white and often tinted with pink; exterior pattern often visible on interior.

Radula (pl. 13, figs 5-7). Inner lateral teeth with medium-sized bases; cusps relatively short, stout. Outer lateral teeth with short bases; inner cusps narrow and pointed, outer cusps broader and more pointed. Marginal teeth small. Radular segment approximately square.

Dimensions

	Height	Length	Width
Holotype of <i>P. calamus</i>	5.75mm	12.15mm	9.95mm
Specimen of <i>A. calamus</i> var. <i>polyactina</i> (? type) (from original description)	7	21	17

Types. *P. calamus*. Holotype (pl. 8, figs 1, 2), BMNH, 70.10.26.156; St. Vincent Gulf, South Australia is given as the locality in the original description but the type is labelled "Port Lincoln, South Australia". *A. calamus* var. *polyactina*. Holotype, SAM, D.13379; Gulf St. Vincent, Sceales Bay and Wallaroo Bay, South Australia, 15 fathoms.

Distribution. Temperate Western Australia along the south coast to southern New South Wales, and in Tasmania. Apparently usually living in the sublittoral.

Remarks. Christiaens (1975b: 93) suggested that *P. calamus* may be related to *P. profunda* (Deshayes, 1863) from the Island of Reunion, in the Indian Ocean. This relationship is here upheld as there is little in the radular or shell characters that would sharply differentiate *P. calamus* from the *P. profunda* series as recognised by Christiaens (1975b). Comparison with the radula and shell of *P. profunda profunda* has not been possible but examination of *P. profunda mauritiana* (Pilsbry, 1891) and *P. profunda albonotata* Smith, 1901 (pl. 13, fig. 9) show them to have similar radulae.

The fine, evenly-spaced radial sculpture distinguishes this subspecies from the next which occurs in north Western Australia.

Patelloida profunda ivani Christiaens, 1975. Pl. 7, figs 17-19, pl. 13, fig. 8.

Patelloida profunda ivani Christiaens, 1975b: 93, pl. 3, fig. 4.

Diagnosis. Shell (pl. 7, figs 17-19). Small, apex at about anterior 1/3, with about 8 moderately strong, widely-spaced radial ribs, each pair with about 4-6 weaker ribs between. Exterior yellowish-orange, primary ribs white. Interior yellowish-white, white spots on margin correspond to ends of primary ribs and short orange-pink lines between these correspond to interspaces between secondary radials. Spatula pale orange, with dark brown spots at edge and a pair of dark brown blotches laterally (description taken from holotype).

Radula (pl. 13, fig. 8). Lateral teeth with short bases and stout, pointed cusps. Cusps of outer and inner lateral teeth approximately equal in size and of similar shape. Marginal teeth short, with very long, spoon-shaped cusps. Radular segment approximately square.

Dimensions

	Height	Length	Width
Holotype	2.65mm	6.9mm (appr.)	5.45mm
Paratype (from original description)	3	7.5	5

Type. Holotype, NMV, F.29551 (pl. 7, figs 17-19), paratypes in Christiaens colln and I. Marrow colln; Dampier, north Western Australia. Part of anterior end of holotype broken.

Distribution. North Western Australia.

Remarks. Only the holotype and topotypes have been available for examination. Christiaens (1975b) regarded this taxon as a subspecies of *P. profunda* (Deshayes, 1863) and, although firm evidence has yet to be advanced to uphold this relationship, the radular characters of *ivani* and the other subspecies of *P. profunda* are certainly similar.

A form of *Collisella onychitis* from Quobba, Western Australia is superficially similar to *P. profunda ivani* in shell characters but has a radula typical of *C. onychitis* (pl. 10, figs 5, 6).

Patelloida saccharina stella (Lesson, 1830). Pl. 8, figs 6-8.

Patella stella Lesson, 1830: 421.

Patella stellaris Quoy & Gaimard, 1834: 356, pl. 71, figs 1-4 (*non Patella stellaris* Röding, 1798, a synonym of *P. saccharina* Linné).

Collisellina paropsis Iredale, 1929: 275; Ripplingale & McMichael, 1961, pl. 3, fig. 12.

Patelloida saccharina stella. — Macpherson, 1955: 243; figs in text, pl. 12, figs 3, 4 (radula) (see for more detailed synonymy).

Patelloida (Patelloida) saccharina. — Christiaens, 1975a: 77 (in part, *non* Linne, 1758).

Diagnosis. Shell (pl. 8, figs 6-8). Ovate, thick, rather large, with several very strong ribs, of

which eight are usually more prominent than others. Apex only slightly anterior and usually eroded. Margin very irregular. Grey or white in colour, with interspaces between the ribs flecked with brown or black, often in a zig-zag pattern. Interior porcellaneous, and grey or white in colour. Spatula usually spotted with characteristic blue or brown. Margin black with white stripes corresponding to external ribs.

Radula. Inner lateral teeth with rounded cusps and medium-sized bases. Outer lateral teeth with very short bases; inner cusps broad and slightly smaller than cusps of inner lateral teeth; outer cusps very small. Marginal teeth long, narrow and curled. Radular segment approximately square.

Dimensions.

	Height	Length	Width
Holotype of <i>C. paropsis</i>	8.02mm	29.40mm	22.06mm
Large specimen (Yeppoon, Queensland)	15.0	43.2	37.5

Types. *P. stella*. Types probably in NHMP; New Zealand (error). *P. stellaris*. Types probably in NHMP; New Ireland. *C. paropsis*. Holotype (pl. 8, figs 6-8), AMS, C.53573; Michaelmas Cay, off Cairns, North Queensland.

Distribution. Northern Australia, from Exmouth in Western Australia to Maroochydore in southern Queensland. Lives in the mid to lower littoral on open rock platforms.

Remarks. Macpherson overlooked *Collisellina paropsis* Iredale, 1929 as an additional synonym of this species. The type is figured here for the first time (pl. 8, figs 6-8).

P. saccharina ranges around tropical Australia to Mauritius and the Andaman Islands, to Papua New Guinea, Indonesia, the Solomon Islands, Fiji, Samoa, New Caledonia, the Philippines, South East Asia and southern Japan. At least three "subspecies" are sometimes recognised. The typical form described from the Philippines ranges through the Central Indo-Pacific region including Indonesia, the Solomons and Fiji. It differs from the "subspecies" *stella* which occurs in Australia, New Caledonia and Papua New Guinea in having very strong primary ribs and very weak or absent secondary ribs. Another "subspecies", *lanx* (Reeve 1855), from southern Japan is sometimes recognised. The Australian form is usually broader than the typical form, usually has the secondary ribs well developed and there are 7-9 primary ribs. The forms *P. saccharina saccharina* (Linné, 1758) and *P. saccharina stella* certainly appear to intergrade, shells from northern Australia often being intermediate or *saccharina*-like. We doubt if the subspecific names will be validated on examination of a larger range of material than is available to us, although it is reasonably clear that there is some, often inconsistent, geographic differentiation.

The Lady Julia Percy Island (Victoria) record cited by Macpherson is clearly based on a mislocalized specimen (the material in the NMV certainly being *P. saccharina stella*). The same author cites a record from northern New South Wales but a single specimen from Nambucca Heads is the only New South Wales specimen that can be located in the NMV (there are none in the AMS collections). It is possible that occasional specimens do occur in northern New South Wales but confirmation is needed.

Patelloida victoriana (Singleton, 1937). Pl. 8, figs 9-12.

Patella hepatica Pritchard & Gatliff, 1903: 194 (*nom. nov. pro Acmaea striata* Pilsbry, 1891: 47, pl. 35, figs. 27-29, (*non* Quoy & Gaimard, 1834); Iredale, 1924: 240 (in part).

Patella victoriae Gatliff & Gabriel, 1922: 152, *nom. nov. pro Patella hepatica* Pritchard & Gatliff, 1903 (*non* Gmelin, 1791).

Patella victoriana Singleton, 1937: 391, pl. 23, fig. 1.

Patelloida victoriana. — Macpherson, 1955: 242, figs in text, pl. 12, figs 1-2 (radula).

Patelloida (*Patelloida*) *victoriana*. — Christiaens, 1975a: 77.

Diagnosis. Shell (pl. 8, figs. 9-12). Moderately large, ovate, moderately elevated, usually eroded or covered with encrusting algae. Apex at about anterior third. Anterior and posterior slopes convex. Sculptured with numerous, irregular, fine riblets which finely but

sharply crenulate margin. Dark or greenish-brown in colour, usually with a white patch at apex due to erosion. Interior white to pale-grey, margin brown.

Radula. Cusp of inner lateral teeth and inner cusps of outer lateral teeth stout, rounded and approximately same size. Outer cusps of outer lateral teeth small and broad with almost straight cutting edges. Bases of both lateral teeth short. Marginal teeth large and hooked. Radular segment broader than long (after Macpherson).

Dimensions

	Height	Length	Width
Holotype (from original description)	7.7mm	23.5mm	17.7mm
Paratype (from original description)	8.5	23.7	18.9
Large specimen (Eagle Hawk Neck, Tasmania)	13.0	31.8	25.6

Types. Holotype, NMV, 70069 and paratype, NMV, 70070; Victoria.

Distribution. Found from Spencer Gulf in South Australia, to Wilson's Promontory in Victoria, and in Tasmania. Lives amongst algae in the sublittoral fringe on exposed coastal platforms.

Remarks. The taxonomic confusion surrounding this species is discussed by Singleton (1937) and Macpherson (1955). Iredale (1924) considered it to be related to *Patellanax peronii* (Blainville) (Patellidae), a conclusion apparently adopted by Oliver (1926) who did not include it in his revision of the "Patelloididae" (= Acmaeidae).

List of recognised taxa and a summary of the major nomenclatural changes in the Australian Acmaeidae

Notoacmea Iredale, 1915 (= *Parvacmea* Iredale, 1915; *Conacmea* Oliver, 1926 and ? *Subacmea* Oliver, 1926)

alta Oliver, 1926 (= *corrosa* Oliver, 1926; *subundulata* auct. (non Angas, 1865). Southern Australia.

conoidea (Quoy & Gaimard, 1834). South Western Australia.

corrodenda (May, 1920). Tasmania and Victoria.

flammea (Quoy & Gaimard, 1834) (= *scabrillirata* Angas, 1865; *subundulata* Angas, 1865

flammea diminuta Iredale, 1924; *septiformis* auct. (non Quoy & Gaimard, 1834)). Temperate Australia.

mayi (May, 1923). Southern Australia.

petterdi (T. Woods, 1876). Tasmania, south eastern and temperate eastern Australia.

Collisella Dall, 1871

mixta (Reeve, 1855) (= *granulosa* Macpherson, 1955) Eastern South Australia, Victoria and Tasmania.

onychitis (Menke, 1843). Temperate Western Australia.

Patelloida Quoy & Gaimard, 1834 (= *Collisellina* Dall, 1871; *Chiazacmea* Oliver, 1926).

alticostata (Angas, 1865). Temperate Australia.

bellatula (Iredale, 1929). North Queensland.

cryptalirata (Macpherson, 1955) (= *ater* Macpherson, 1955). Tropical eastern Australia and northern Australia.

heteromorpha (Oliver, 1926). Queensland.

insignis (Menke, 1843). (= *crucis* T. Woods, 1876; *flammea* auct. (in part) (non Quoy & Gaimard, 1834)). South Western Australia to South Australia and Tasmania.

latistrigata (Angas, 1865) (= *marmorata* T. Woods, 1876; *submarmorata* Pilsbry, 1891). South-eastern and eastern temperate Australia including Tasmania.

mimula (Iredale, 1924) (= *flammea queenslandiae* Oliver, 1926; *flammea marrowi* Christiaens, 1975). Tropical Australia and temperate eastern Australia.

mufria (Hedley, 1915) (= *insignis cavilla* Iredale, 1924). Temperate eastern Australia and the south coast.

nigrosulcata (Reeve, 1855) (= *patellavecta* Verco, 1912). South Western Australia.

saccharina stella (Lesson, 1830) (= *paropsis* Iredale, 1929). Tropical eastern and northern Australia.

profunda calamus (Crosse & Fischer, 1864) (= *polyactina* Verco, 1912). Southern and south Western Australia.

profunda ivani Christiaens, 1975. North Western Australia.

victoriana (Singleton, 1937). Southern Australia including Tasmania.

N.B. Species included in the genus group taxa *Asteracmea*, *Naccula* and *Simplacmaea* are not included in this revision.

ADDITIONAL TAXONOMIC NOTES

Collisella (?) septiformis (Quoy & Gaimard, 1834). Pl. 3, figs 7-15.

Patelloida septiformis Quoy & Gaimard, 1834: 362, pl. 71, figs 43-44.

Notoacmea (Notoacmea) septiformis septiformis. — Oliver, 1926: 572 (in part).

Collisella (Notoacmea) septiformis. — Christiaens, 1975b: 103.

Dimensions

	Height	Length	Width
Possible syntypes	3.80mm	16.00mm	12.75mm
	4.40	16.10	12.08
	4.70 (approx)	15.53	12.75
	4.25	17.50	14.36
	4.54	13.86	11.87
	4.9 (approx)	17.90	14.48

Types. Possible syntypes (9) (pl. 3, figs 7-15) NHMP; "King George Sound" (? = Tonga).

Remarks. None of the 9 presumed syntypes agrees exactly with the original illustration but the one which is closest is marked "Tonga". Two others are also marked but the writing is indecipherable. The label gives the locality as King George Sound but no specimens seen from that locality, or from any other Australian locality, agree with this species. All the specimens appear to be a single species with fine, distinct radial lirae externally which are alternately weak and strong. Both the primary and secondary lirae are very finely scabrous. The interior is white to bluish-white with a white to brown centre. The internal margins are variable with narrow, dark markings from the exterior colour showing through. The exterior coloration is also variable; narrow to broad rays of brown with a reticulate or lace-like pattern usually predominating over most of the shell.

A search of several museums (NMV, AMS, BMNH and several European museums) has failed to locate any comparable specimens or any similar material from Tonga. The most similar Australian species is *Notoacmea flammea* which differs in its finer, lace-like markings, the less distinct radial markings, more opaque-white interior, more distinctly separated spatula, usually slightly thinner shell, and different external sculpture. In *N. flammea* the external striae are approximately equal in strength and are nodulose rather than scabrose.

The species here taken to be *Patelloida septiformis* is probably a species of *Collisella* but confirmation of its generic position will have to await the location of living material.

Notoacmea elongata (Quoy & Gaimard, 1834). Pl. 3, figs 16-19.

Patelloida elongata Quoy & Gaimard, 1834: 358, pl. 71, figs 12-14; Oliver, 1926: 573.

Acmaea daedala Suter, 1907: 328, pl. 27, figs 30-32.

Notoacmea (Parvacmea) daedala. — Oliver, 1926: 576, text fig. F.

Collisella (Parvacmea) daedala. — Christiaens, 1975b: 105.

Dimensions

	Height	Length	Width
Syntypes	1.66mm	6.15mm	4.7mm
	—	5.9	4.1
	1.4	4.8	3.5
	1.15	4.64	2.8 (approx.)

Types. 4 syntypes, NHMP (pl. 3, figs 16-19) "King George Sound" — error for New Zealand.

Remarks. The 4 syntypes of *P. elongata* agree in every particular with *N. daedala* (Suter) from New Zealand. Suter's species is the type species of Iredale's subgenus *Parvacmea*. Both *N. elongata* and *N. helmsi* (Smith), another New Zealand species, appear to be closely related to *N. flammea* which Oliver (1926) considered to be a typical *Notoacmea* (as *N.*

septiformis). Juvenile *N. flammea* differ from *N. elongata* in having rather widely spaced, distinctly granulose radial threads instead of fine radial striae and *N. flammea* has a different, coarser colour pattern.

Acmaea transparens Test, 1945: 96.

Types. Two syntypes, NHMB; "Australia".

Remarks. The two broken types are specimens of *Naccula punctata* (Quoy & Gaimard, 1834) (Acmaeidae; see Oliver, 1926 : 566), as suggested by Christiaens (1975b : 106).

Acmaea eccentrica Test, 1945 : 95.

Types. Specimens labelled 'holotype' and 9 'paratypes' have been examined. 14 syntypes were cited in the original description. NHMB; "Sydney and Port Jackson Australia. 'Rosto de Caô'". The 'holotype' is labelled 'Sydney'. Because a holotype was not designated in the original description the specimen labelled as the holotype is here designated the lectotype.

Dimensions. Lectotype. Height 1.5mm; length 3mm; width 2.1mm.

Remarks. The lectotype and 8 of the paralectotypes are a species of *Cocculina* (Cocculinidae) and one paralectotype is *Pugillaria stowae* (Verco) (Siphonariidae). This latter specimen is the only one with the golden "freckles" noted in the description. Christiaens (1975b : 106) has erroneously suggested that *A. eccentrica* is *Simplacmaea stowae* (Verco).

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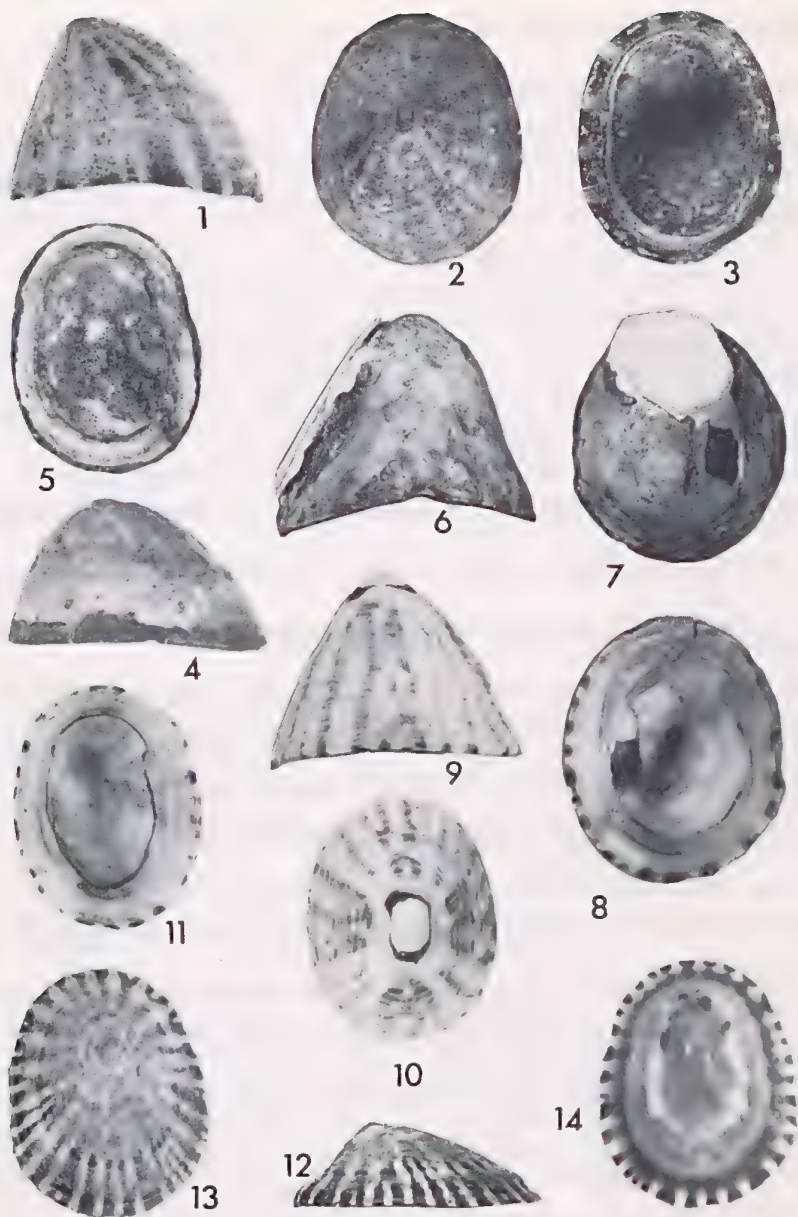


Plate 1.

1-5. *Notoacmea alta* Oliver. 1-3. Holotype. Height 4mm, length 6mm, width 5mm. 4, 5. Holotype of *N. corrosa* Oliver. Height 5mm, length 8.5mm, width 6.5mm

6-11. *Notoacmea conoidea* (Quoy & Gaimard). 6-8. Holotype. Height 11.4mm, length 13.74mm, width 11.32mm. 9-11. Albany, south Western Australia (AMS, C.96705). Height 9.5mm, length 13.16mm, width 10.05mm.

12-14. *Notoacmea corrodenda* (May). Paralectotype (AMS, C.45952). Height 4.54mm, length 13.57mm, width 10.7mm.



Plate 2.

1-18. *Notoacmea flammea* (Quoy & Gaimard). 1-3. Lectotype. Height 4.0mm, length 11.25mm, width 9.6mm. 4-6. Paralectotypes, 4-6. Height 3.12mm, length 10.24mm, width 8.26mm. 7-9. Height 3.5mm, length 10.9mm, width 8.7mm. 10-12. Height 4.21mm, length 11.16mm, width 9.39mm. 13-15. Holotype of *Acmaea subundulata* Angas. Height 5.7mm, length 14.75mm, width 11.7mm. 16-18. Topotype of *Notoacmea flammea diminuta* Iredale, Bottle and Glass Rocks, Sydney Harbour, New South Wales (AMS, C.49539). Height 3.22mm, length 10.7mm, width 8.75mm.

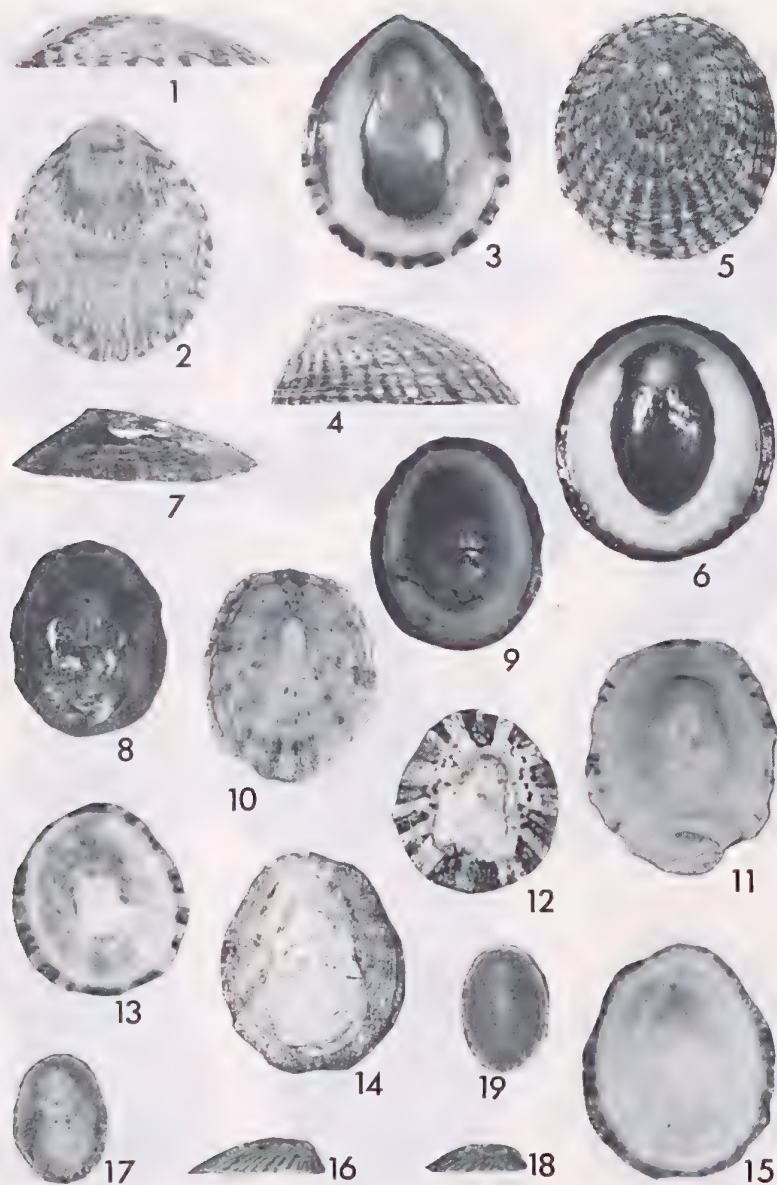


Plate 3.

1-3 *Notoacmea mayi* (May) Lectotype. Height 4.55mm, length 23.1mm, width 18.75mm
 4-6. *Notoacmea petterdi* (I. Woods). Lakes Entrance, Victoria (AMS, C.112760), Height 8.75mm, length 22.1mm, width 19.55mm.
 7-15. *Collisella (?) septiformis* (Quoy & Gaimard). Possible syntypes, NHMP 7-9. Height 3.8mm, length 16.0mm, width 12.75mm, 10, 11. Height 4.25mm, length 17.5mm, width 14.36mm, 12-13. Height c.4.7mm, length 15.53mm, width 12.75mm. 14, 15. Height c.4.9mm, length 17.9mm, width 14.48mm. 16-19. *Notoacmea elongata* (Quoy & Gaimard). Syntypes. 16, 17. Height 1.66mm, length 6.15mm, width 4.7mm. 18, 19. Length 5.9mm, width 4.1mm.

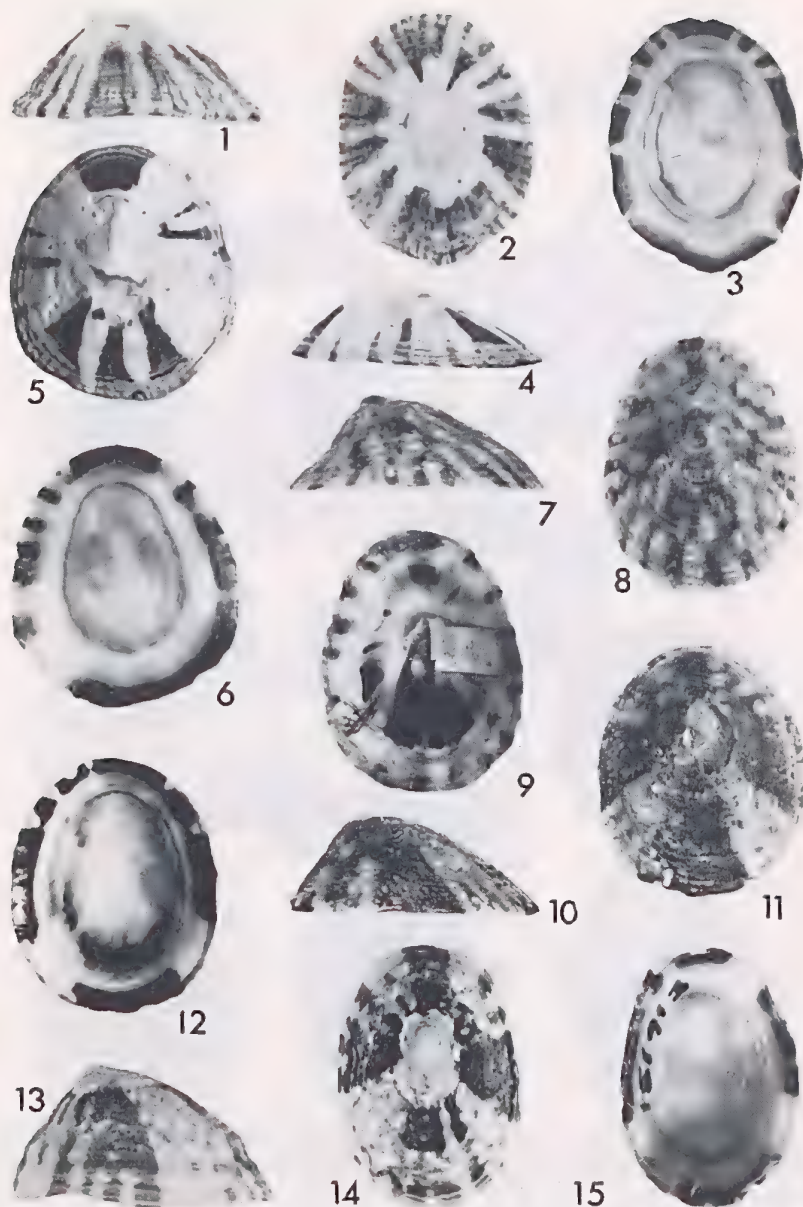


Plate 4.

1-6. *Collisella onychitis* (Menke). 1-3. Thomson Bay, Rottneest Island, Western Australia (AMS, C.112758). Height 8.37mm, length 21.3mm, width 15.96mm. 4-6. Cape Riche, south Western Australia (AMS, C.112757). Height 3.9mm, length 13.3mm, width 11.8mm.

7-15. *Collisella mixta* (Reeve). 7-9. Lectotype. Height 6.1mm, length 16.6mm, width 12.7mm. 10-12. Paralectotype. Height 6.67mm, length 17.5mm, width 14.04mm. 13-15. Holotype of *Notoacmea granulosa* Macpherson. Height 7.64mm, length 14.46mm, width 10.2mm.



Plate 5.

1-6. *Patelloida alticostata* (Angas). 1-3. Portsea, Victoria (AMS C.90737). Height 11.9mm, length 28.9mm, width 23.5mm. 4-6. Boat Harbour, near Cronulla, New South Wales (AMS, C.84424). Height 14mm, length 40.1mm, width 34.85mm.

7-9. *Patelloida bellatula* (Iredale). Paratypes. 7. Height 5.3mm, length 15.24mm, width 10.95mm. 8. Height 4.1mm, length 12.7mm, width 9.35mm, 9. Height 2mm, length 8.02mm, width 5.5mm.

10-15. *Patelloida cryptalirata* (Macpherson). 10-12. Paratype. Height 3.4mm, length 10.3mm, width 8.9mm. 13-15. Holotype of *Chiazacmea ater* Macpherson. Height 2.75mm, length 11mm, width 8.7mm.

16-18. *Patelloida heteromorpha* (Oliver). Holotype. Height 8mm, length 18.05mm, width 15.93mm.

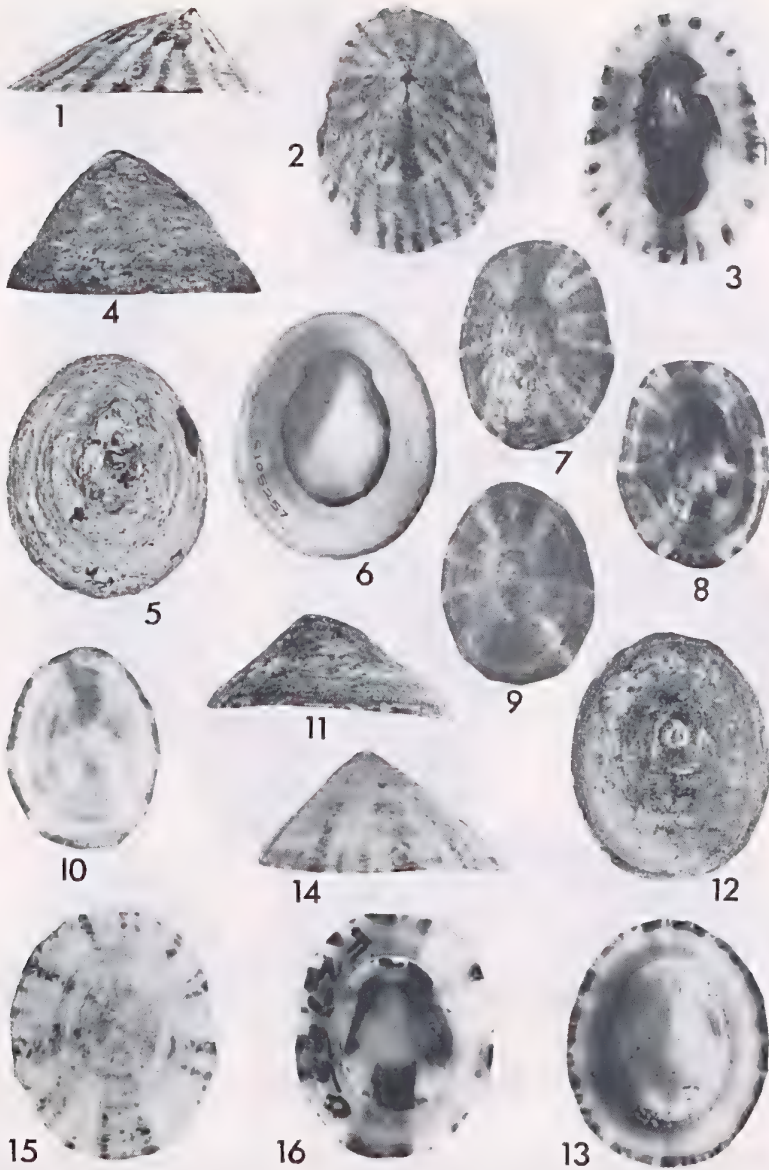


Plate 6.

1-6. *Patelloida insignis* (Menke). 1-3. Augusta, south Western Australia (AMS, C.112761). Height 8.25mm, length 20.2mm, width 15.3mm. 4-6. Lectotype of *Acmaea crucis* T. Woods. Height 17.45mm, length 31.1mm, width 25mm.

7-16. *Patelloida mimula* (Iredale). 7, 8. Lectotype of *Patella jacksoniensis* Reeve non Lesson = *Notoacmea mixta mimula* Iredale. Height 7.3mm, length 19.5mm, width 14.3mm. 9, 10. Paralectotype of *P. jacksoniensis* Reeve. Height 6.2mm, length 18.85mm, width 14.15mm. 11-13. Holotype of *Chiazacmea flammea queenslandiae* Oliver. Height 5.4mm, length 13.73mm, width 10.01mm. 14-16. Holotype of *Patelloida flammea marrowi* Christiaens. Height 4.7mm, length 9.5mm, width 7.6mm.

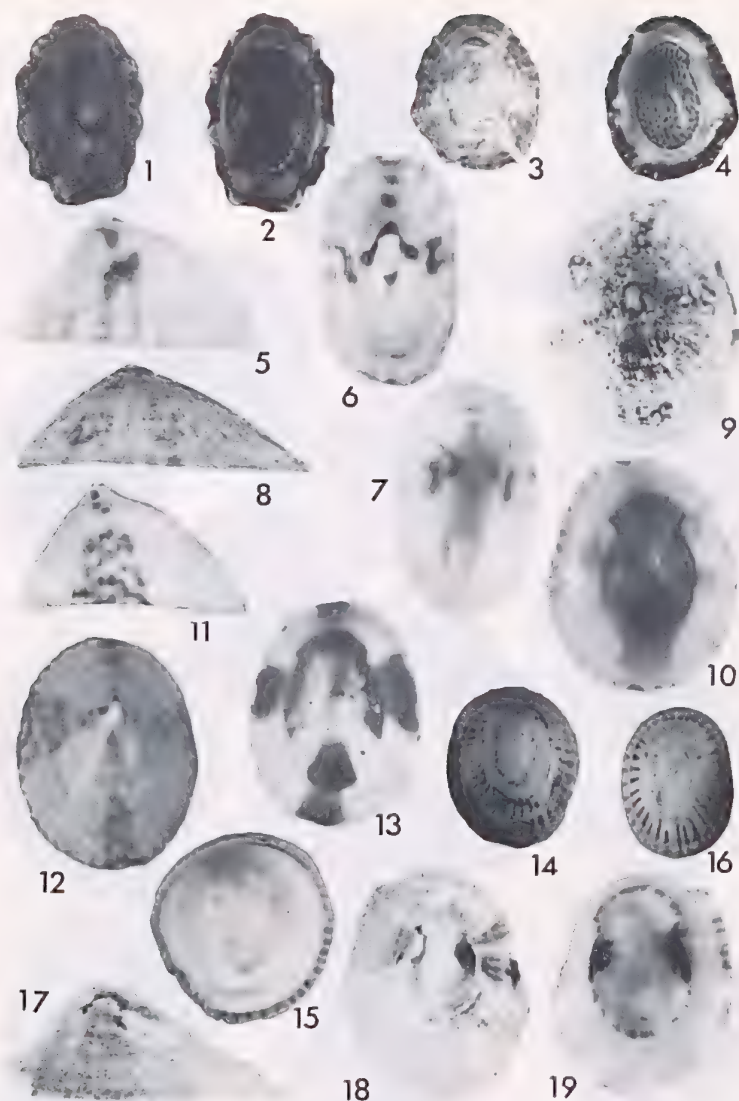


Plate 7.

1-4. *Patelloida latistrigata* (Angas). 1, 2. Holotype. Height 6.0mm, length 17.8mm, width 11.7mm. 3, 4. Lectotype of *Acmaea marmorata* var. *submarmorata* Pilsbry. Height 6.3mm, length 16.15mm, width 13.4mm.

5-13. *Patelloida mufria* (Hedley). 5-7. Lectotype. Height 2.8mm, length 5.54mm, width 3.37mm. 8-13. Long Reef, Collaroy, New South Wales (AMS, C.112762). 11-13. Height 4.55mm, length 12.56mm, width 10mm. 7-9. Height 4.27mm, length 7.6mm, width 6mm.

14-16. *Patelloida nigrosulcata* (Reeve). 14, 15. Paralectotypes. 14. Height 15.4mm, length 29.15mm, width 24.9mm. 15. Height 21.6mm, length 39mm, width 31mm. 16. Lectotype. Height 8.9mm, length 28.6mm, width 20.7mm.

17-19. *Patelloida profunda ivani* Christiaens. Holotype. Height 2.65mm, Length c.6.9mm, width 5.45mm.

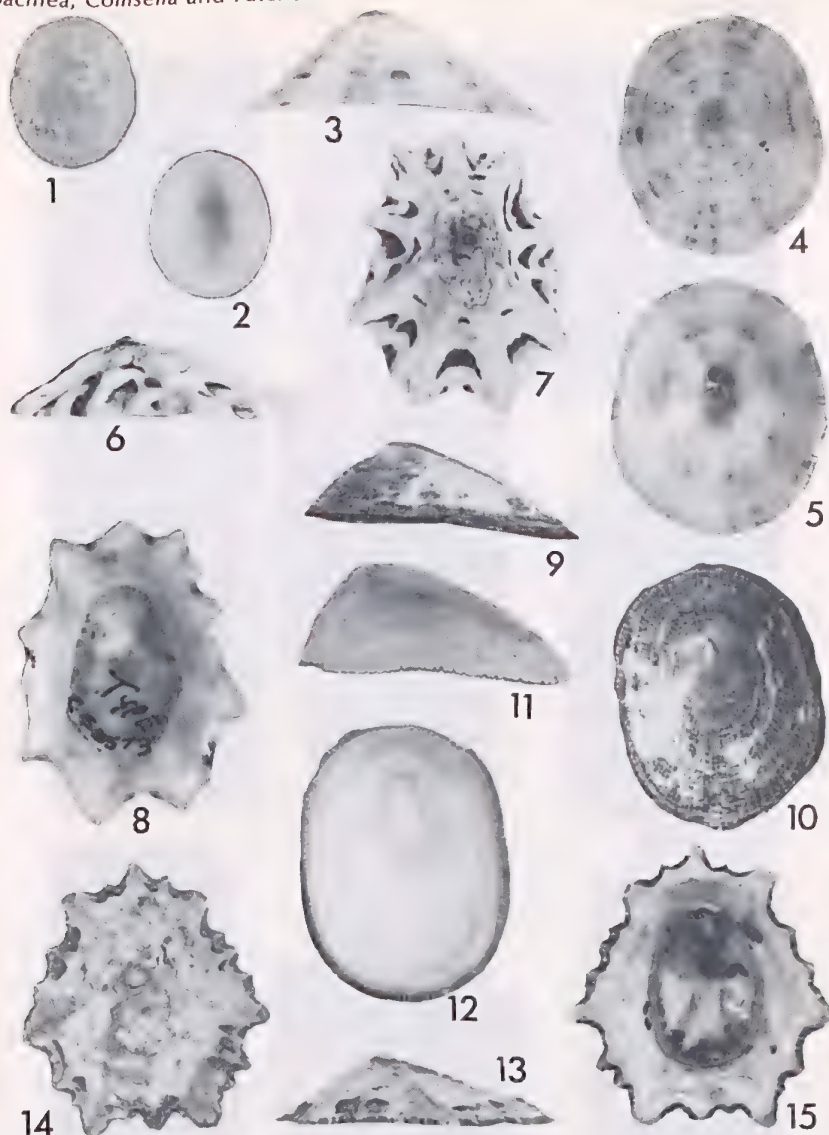


Plate 8.

1-5 *Patelloida profunda calamus* (Crosse & Fischer). 1, 2. Holotype. Height 5.75mm, length 12.15mm, width 9.95mm. 3-5. Windy Harbour, south Western Australia (AMS, C.112763); a large specimen resembling the type of *A. calamus* var. *polyactina* Verco. Height 5.6mm, length 15.7mm, width 13.07mm.

6-8. *Patelloida saccharina stella* (Lesson). Holotype of *Collisellina paropsis* Iredale. Height 8.02mm, length 29.4mm, width 22.06mm.

9-12. *Patelloida victoriana* (Singleton). 9, 10. Tullaberga Island, Mallacoota Inlet, Victoria (AMS, C.93397). Height 6.2mm, length 21.2mm, width 15.85mm. 11-12. Cape Sorell, west coast, Tasmania (AMS, C.112759). Height 11.87mm, length 29.72mm, width 22.13mm.

13-15. *Lottia* (?) *costata* Holotype. Height 8.5mm, length 35.5mm, width 31.84mm.



Plate 9.

1-4. *Notoacmea alta* (Oliver). 1, 2. Port Lonsdale, Victoria. Small black form on shells of *Brachidontes* (Stub No. 643, C.112970) x 310. 3, 4. Eaglehawk Neck, south Tasmania. (Stub No. 644, C.112971) x 370.

5-10. *Notoacmea flammea* (Quoy & Gaimard). 5, 6. Two Peoples Bay, south Western Australia (Stub No. 679, C.112972) x 310. 7, 8. Vaucluse, Sydney, New South Wales. Flattened shells from sheltered shore (Stub No. 714, C.112973) x 310. 9, 10. Eaglehawk Neck, south east Tasmania (Stub No. 715, C.112990) x 240.

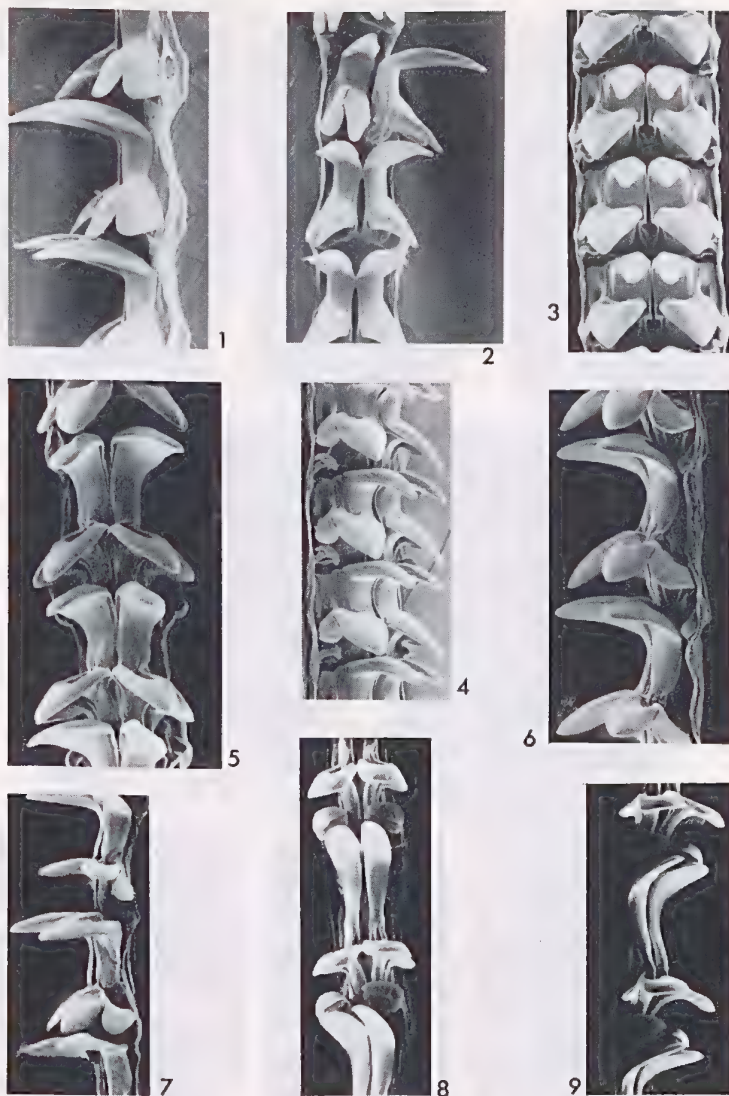


Plate 10.

1, 2. *Notoacmea petterdi* (T. Woods). Vaucluse, Sydney, New South Wales (Stub. No. 31, C.112974) x 180 (fig. 1), x 160 (fig. 2).

3, 4. *Patelloidea cryptalirata* (Macpherson). Mossman, north Queensland (Stub No. 910, C.113556) x 160.

5-7. *Collisella onychitis* (Menke). 5, 6. Point Quobba, Western Australia (Stub No. 912, C.113567) x 180. 7. Dunsborough, south Western Australia (Stub No. 656, C.112975) x 120.

8, 9. *Patelloidea latistrigata* (Angas). Frederick Henry Bay, south east Tasmania (Stub No. 717, C.112980) x 160.

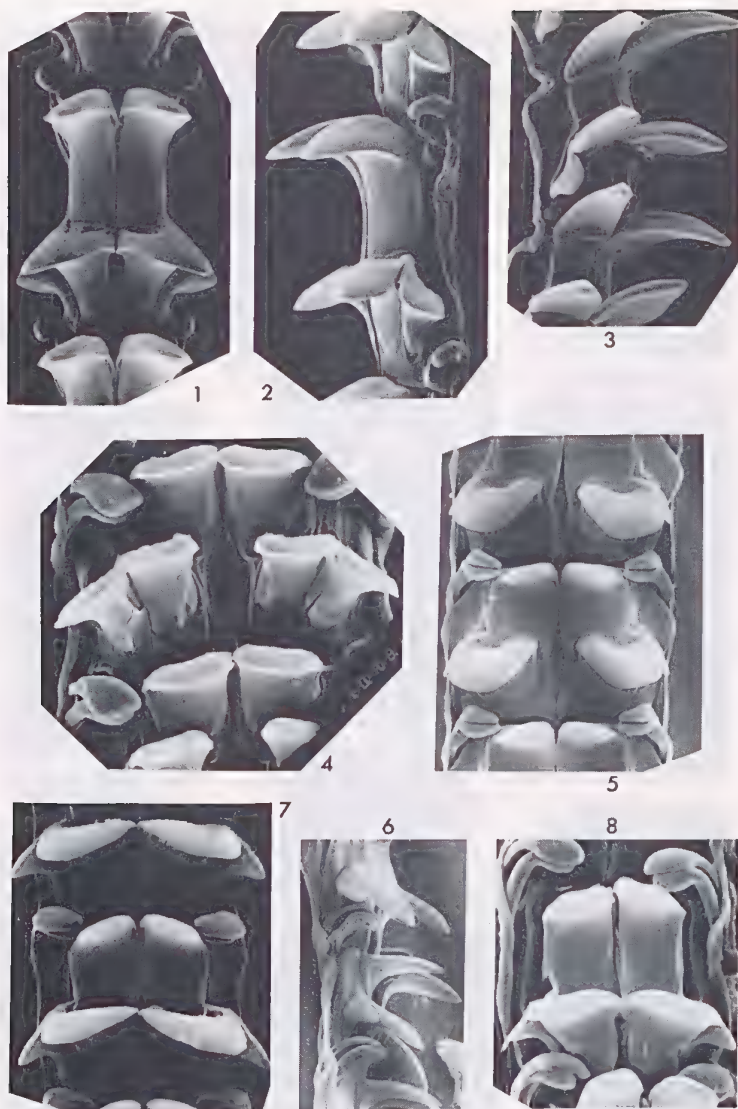


Plate 11.

1, 2. *Collisella mixta* (Reeve). Port Campbell, Victoria (Stub No. 684, C.112976) x 210.

3. *Notoacmea corrodenda* (May). Eaglehawk Neck, south east Tasmania (Stub No. 649, C.112978) x 210.

4. *Patelloida bellatula* (Iredale). Yonge Reef (east of Lizard Island), north Queensland (Stub No. 640, C.112977) x 360.

5-8. *Patelloida mimula* (Iredale). 5, 6. Tambourine Bay, Sydney Harbour, New South Wales (Stub No. 29, C.112981) x 170. 7, Maningrida, Northern Territory (Stub No. 677, C.112982) x 200. 8. Dampier, north western Australia (Stub No. 636, C.112983) x 280.

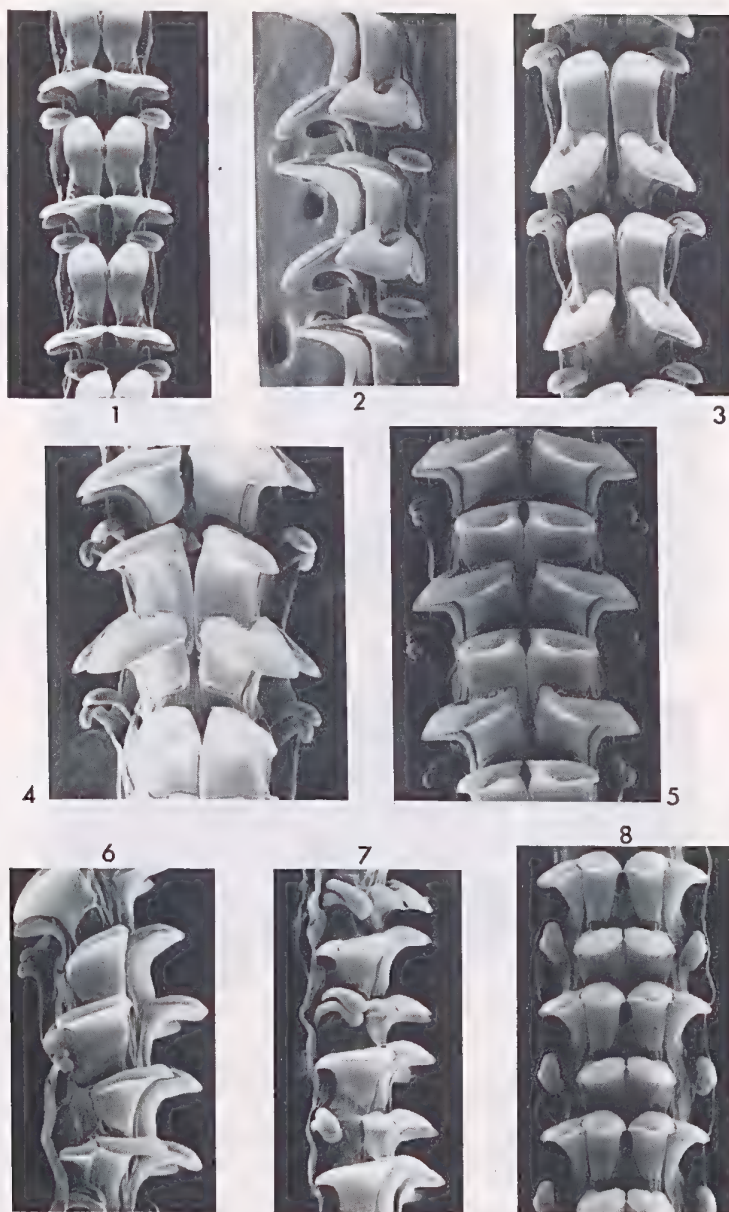


Plate 12.

1-3. *Patelloida heteromorpha* (Oliver). 1. Tannum Sands, near Gladstone, Queensland (Stub No. 907, C.113553) x 160. 2, 3. Mossman, North Queensland (Stub No. 908, C.113554) x 160. 4-6. *Patelloida insignis* (Menke). 4. Cape Naturaliste, south Western Australia (Stub No. 909, C.113555) x 190. 5, 6. Eaglehawk Neck, south Tasmania (Stub No. 655, C.112979) x 100. 7, 8. *Patelloida nigrosulcata* (Reeve). Fremantle, Western Australia (Stub No. 662, C.112985) x 100.

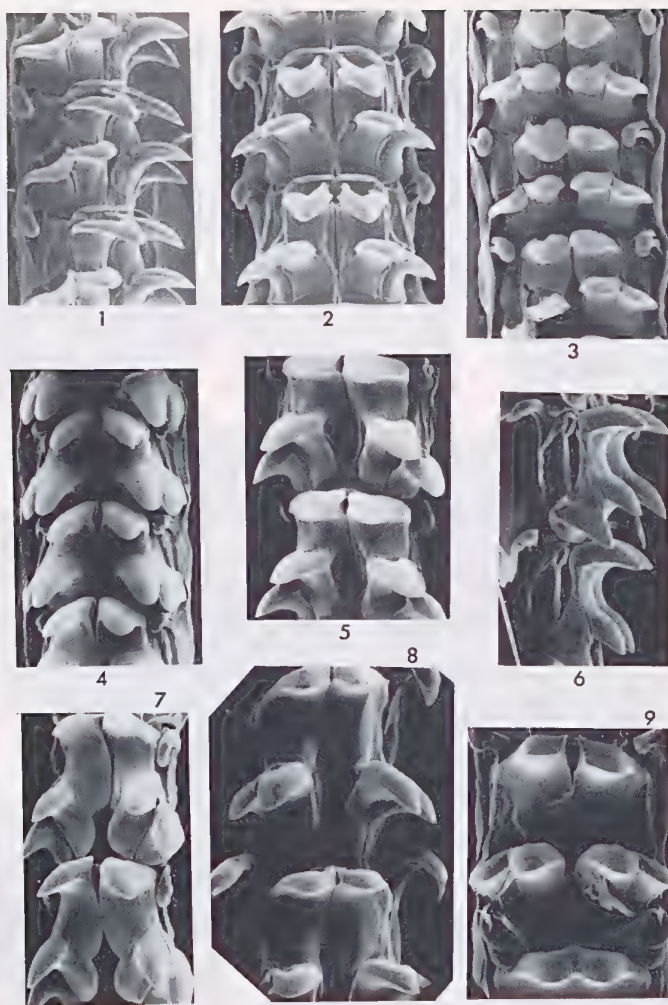


Plate 13.

1-4. *Patelloidea mufria* (Hedley). 1, 2. Balmoral, Sydney, New South Wales. Small, laterally compressed, high spired form living subtidally on shells of *Thais orbita* (Gmelin) Stub No. 911, C.113557) x 310. 3. Mallacoota, Victoria. Large form living on exposed rocks. (Stub No. 653, C.112984) x 170. 4. Cape Banks, Botany Bay, New South Wales. Large form, living on exposed rocks (Stub No. 30, C.113558) x 240.

5-7. *Patelloidea profunda calamus* (Crosse & Fischer). 5. Dunsborough, Western Australia (Stub No. 678, C.112986) x 160. 6, 7. American River, south Western Australia living subtidally on shells (Stub No. 632, C.112987) x 260.

8 *Patelloidea profunda ivani* Christiaens. Dampier, north Western Australia (topotype) (Stub No. 633, C.112988) x 310.

9. *Patelloidea profunda albonotata* (Smith). Natal, South Africa (Stub No. 676, C.112989) x 240.

The Egg Capsules of *Lepsiella vinosa* (Lamarck, 1882) (Muricidae : Thaidinae)

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SUMMARY

Egg capsules of *Lepsiella vinosa* are described and compared with published accounts of those of other Australian muricids. Capsules of *L. vinosa* are laid separately in the intertidal zone, are lens-shaped, and approximately 4 mm in diameter and 1.4 mm high. Capsules contain about 7 eggs which hatch as young snails. The breeding biology of *L. vinosa* is compared with that of other Australian and New Zealand muricids.

INTRODUCTION

The only Australian thaid egg capsules described are those of *Cronia avellana* (Reeve, 1846) and *C. pseudamygdala* (Hedley, 1903) by Phillips, (1975); *Thais orbita* (Gmelin, 1971) by Hedley (1906) and Phillips (1969); and *Morula marginalba* (Blainville) by Anderson (1965). Egg capsules and breeding biology of the New Zealand thaid *Lepsiella scobina* (Quoy and Gaimard) were described by Graham (1941) and Fearon (1962). *Lepsiella vinosa* (Lamarck, 1882) is a small prosobranch which occurs in the littoral zone on rocky shores around southern Australia (Synnot and Wescott, 1976). *L. vinosa* ranges from Jervis Bay, New South Wales, to Cockburn Sound in Western Australia, (MacPherson and Gabriel, 1962; Synnot, unpub. data).

This paper describes the egg capsules, number of eggs per capsule, and hatching time of *L. vinosa*.

MATERIALS AND METHODS

Egg capsules of *L. vinosa* were collected from the following localities: Flinders (11/8/74), Apollo Bay (10/8/76), Point Roadknight (23/8/77), Corinella (20/9/77), Bird Rock, Western Port Bay (1/5/78), and Barry's Beach, Phillip Island (11/12/78). Capsules were identified by reference to egg capsules laid by *L. vinosa* in the laboratory, and specimens in the F.V. Murray spawn collection (National Museum of Victoria). The specimens from Flinders were maintained in seawater (approx. 14°C) in the laboratory under an artificial tidal cycle whose periodicity was similar to that in the field, and embryonic development was observed daily.

The height, diameter, and width of the hatching aperture of each capsule were measured using a Zeiss Binocular microscope with a calibrated eyepiece graticule. Values are given in the text as mean \pm S.E.

RESULTS

Egg capsules of *L. vinosa* were observed in the field between May and December on sheltered coasts, and between August and December on exposed coasts (Flinders, Apollo Bay). The egg capsules of *L. vinosa* are laid separately and are cemented to the substrate. Capsules were found in and around colonies of the encrusting serpulid worm *Galeolaria caespitosa*, under rocks, and in the empty valves of the mussel *Brachidontes rostratus*. The capsules are lens-shaped, and have a flat semi-transparent basement membrane (Fig 1.). The upper dome is translucent, except for a circular transparent area through which hatching occurs. Two suture lines run from this central area to the edge of the capsule. Measurements of 11 capsules are: diameter 4.2 ± 0.2 mm; height 1.4 ± 0.03 mm; hatching aperture 0.98 ± 0.02 mm; eggs per capsule, 7.5 ± 0.41 (range 6-9). The eggs are suspended in a colourless fluid, are light orange in colour, and have a diameter of $901 \pm 6.5 \mu$. Only one of the capsules collected from Flinders (11/8/1974) and maintained in the laboratory hatched; the remaining five turned deep purple, and were found to be infected by nematodes. The time period from collection to hatching was 34 days, and the size of young at hatching (largest dimension) was 2.14 ± 0.04 mm ($n=5$). This capsule contained nine eggs when collected, but no remains of the other four eggs were found in the capsule prior to hatching. The eggs which did not develop may be "nurse" eggs which were eaten by the surviving individuals. The young emerged as crawling juveniles.

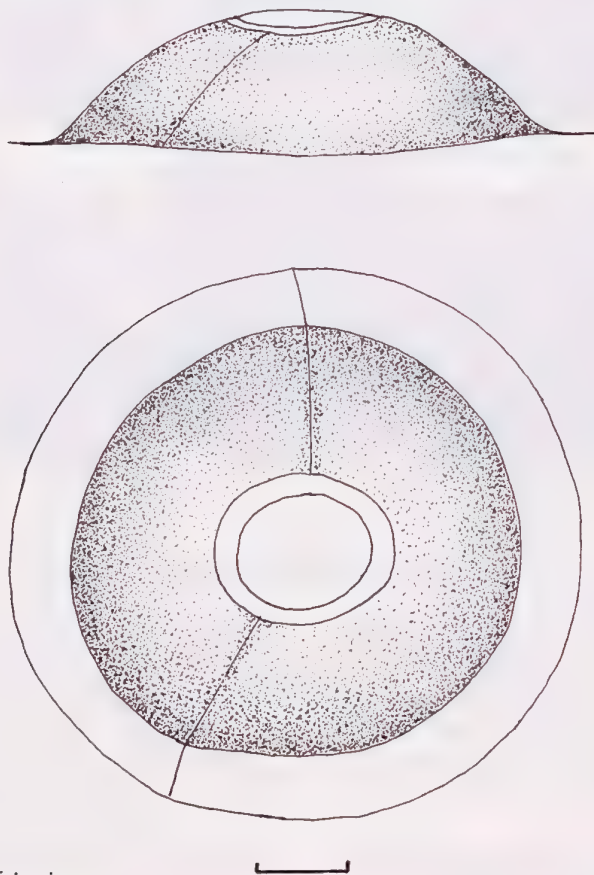


Fig. 1.

Egg Capsule of *L. vinosa*.
(Scale bar = 1mm.)

DISCUSSION

Egg capsules of *L. vinosa* closely resemble those of *Bedevea hanleyi* and *Bedevea paivae* (Muricidae: Muricinae) described by Anderson (1965) and Black (1976) respectively, and are similar to those of *Cronia avellana* described by Phillips (1975). The capsules of these species can be distinguished by the number of eggs present (6-9 eggs/capsule for *L. vinosa*; 50-70 for *B. hanleyi*; 54-106 for *C. avellana*), and by the symmetry of the sutural lines on the upper surface (asymmetrical in *L. vinosa*; symmetrical in *B. hanleyi*; reduced or absent in *C. avellana*).

The collection dates for egg capsules of *L. vinosa* indicate an eight month difference in reproductive period on Victorian shores. As the spawning behaviour of thaid molluscs has been correlated with food availability (Spight and Emlen, 1976), populations of *L. vinosa* which feed in or close to spawning areas (Barry's Beach, Bird Rock) may spawn throughout the year. However, where areas to lower intertidal spawning areas (Flinders) (Synnot, pers. obs.) frequency of spawning may be reduced.

The laboratory observations suggest that *L. vinosa* (Thaidinae) and *Bedevea hanleyi* (Muricinae) are the only Australian muricids in which direct development and nurse eggs are known to occur. *Lepsiella scobina* of New Zealand also displays these characteristics (Fearon, 1965). This is consistent with the argument of Spight (1977), that among muricids of rocky shores, species at high latitudes metamorphose before hatching (*Lepsiella*, *Bedevea*), whilst more tropical species (*Morula*, *Cronia*) have planktonic larvae. Further studies of Australian muricids, particularly those with wide latitudinal ranges, should enable muricid reproductive patterns to be more fully appraised.

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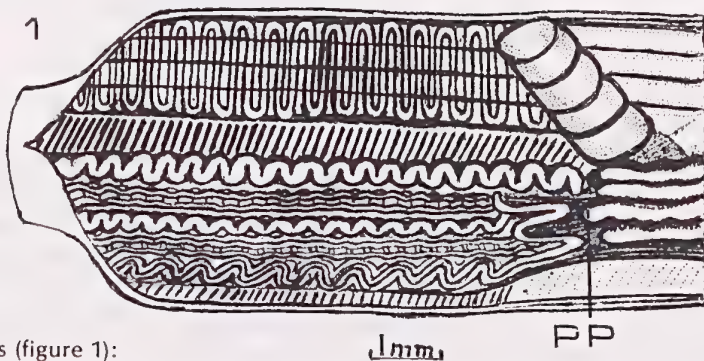
The author thanks G. Parry and G. Quinn for assistance with field observations and records. Dr. G.F. Watson read and criticized the manuscript. Dr. Brian Smith made the Florence Murray spawn collection available.

Notes on *Helicarion rubicundus* (Pulmonata : Helicarionidae)

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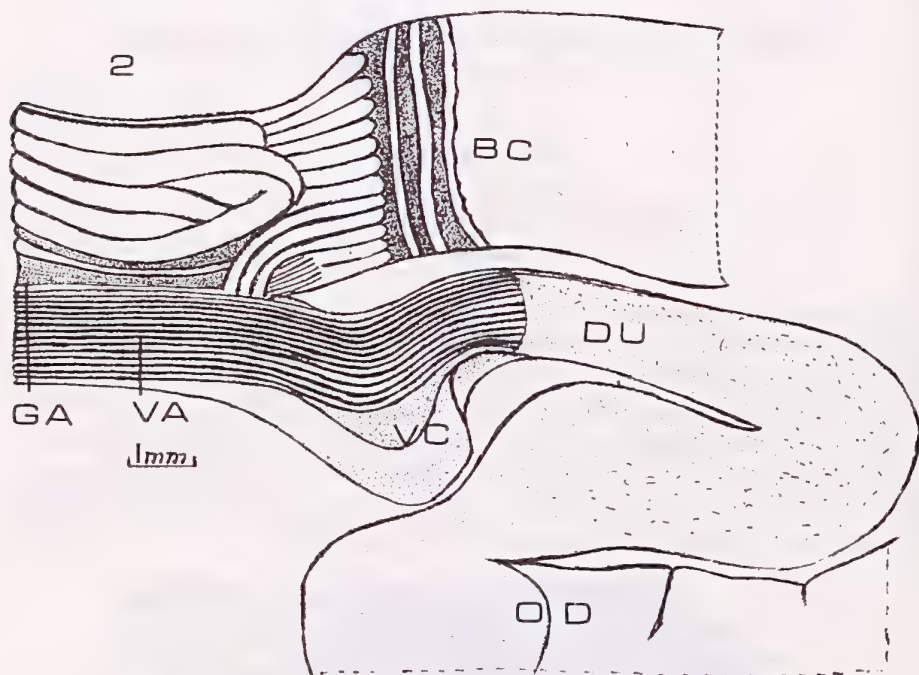
Study of *Helicarion* genitalia has emphasized the need for dissection and study of the micro-structure in detail. It has been apparent that the description of the penis and bursa copulatrix duct in *Helicarion rubicundus* Dartnall & Kershaw, 1978 is inadequate for comparative purposes. In addition the penial papilla is incorrectly described as a verge. It is compound, and not the simple digitiform structure shown in the figured section. The species is described as possessing a retractor caecum which was thought to be degenerate. Further study has shown this structure to be simply the bulging, sometimes unusually shaped base of the retractor muscle, and is not in fact a caecum. The retractor muscle base has various differences in structure in the genus, ranging from very simple to the complex as in this instance. In no case has a true caecum been found.



The penis (figure 1):

The original description of the internal structure (Dartnall & Kershaw, 1978, p.4) refers to lamellate transverse ridges. This arose from the appearance as revealed by a simple longitudinal section. The technique of sectioning the penis to reveal the whole internal surface as figured here, indicates the important differences observed. The structure consists, of longitudinally oriented transverse folds with short, minor transverse ridges, accentuating the effect. The broad tight folds noticeable in the figure are slit into longitudinal rows of papillae. These are apparent when the penis is everted. The complexity of the ornament is increased by the presence of very low close slightly wavy ridges between the bold folded ridges. The central pair in each case is joined transversely at frequent intervals.

The penial papilla complex consists of four contorted digitiform processes the most prominent of which is raised into the small rounded bulge originally observed. This bulge is separated from the wall of the penis and is regarded as the stimulatory part of the papilla. A relatively large segmented ridge is situated diagonally adjacent to the papilla. The function of this structure or how often it is present is not known. It occupies a situation similar to that of tight lines of papillae or ridges observed in certain other morphs. It may have some stimulatory function and may be essentially similar to but lacking the discrete divisive structure encountered in the morphs mentioned.



The bursa copulatrix duct (figure 2).

The bursa copulatrix has not been adequately described. The duct is described as possessing a small vestibule which is due to the broadening and flattening of the initial pilaster ridges. These are curiously and uniquely curved at this point. The following series of ridges tend to radiate, almost fan-like, into the bursa chamber entrance. The longitudinal vaginal ornament is in fact very closely lamellate in structure. It enters a region since described as a vaginal chamber which, at least in part, includes a small diverticulum. The ornament then passes into the uterine duct. In this species as originally noted, this duct has a unique convolution still unobserved in any other morph.

Abbreviations used:

DU uterine duct, BC bursa copulatrix, GA genital atrium, OD spermathecal complex, PP penial papilla, VA vagina, VC vaginal chamber.

REFERENCE

Dartnall, A.J. & R.C. Kershaw, 1978. Description of a new species of *Helicarion* (Stylomatophora : Helicarionidae) in Tasmania. *Rec. Queen Vict. Mus.* 62 : 1-18, pls. 1-5.

GONDWANALAND CONNECTIONS IN THE TERRESTRIAL MOLLUSCS OF AFRICA AND AUSTRALIA¹

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SUMMARY

Africa and Australia share only two Gondwanaland families, the Rhytididae and Charopidae. In a bicontinental pattern the former are rather diverse in the Australian Region and only sparsely represented in Africa; the latter are of somewhat comparable diversity in both continents, but appear to be very diverse elsewhere (e.g., New Zealand), while exhibiting a tri continental pattern. The evolutionary success of these and other Gondwanaland families has been markedly poor in Africa as compared to that in the other remnants of Gondwanaland. This may be explained by the island history of Africa and its subsequent contact with Eurasia (Laurasia); once this was established the vigorous and diverse Eurasian elements started invading Africa from the north replacing the Gondwanaland —elements or frustrating their northward dispersal. Both Australia and South America remained comparatively much more isolated, so that the Gondwanaland elements retained or established a comparatively much more dominant position.

Biogeography in general has recently received new impulses mainly as regards its theoretical background such as the new phylogeny and the stunning geological contributions known as the complex of continental drift, plate tectonics and palaeomagnetism. Biogeography of land molluscs is still in its infancy because of factors such as the large number of species involved, poor knowledge of their relationships consequent on limited anatomical data and as yet poorly understood distribution patterns. The biogeography of terrestrial gastropods has virtually entered a new era since Solem's paper (1959) on the New Hebrides.

Africa south of the Sahara harbours a rich fauna of land snails, recently estimated at ca. 6000 species (Van Bruggen, 1977). The species of the southern parts of the continent are of particular interest since their distribution essentially reflects a bipolar pattern, namely elements of northern origin intimately intermixed with elements of southern origin (Van Bruggen, 1969). Most of the southern elements may be termed Gondwanaland elements. Gondwanaland families are here defined as families that mainly show a distribution on one or more fragments of ancient Gondwanaland.

Some southern distribution patterns in Africa do not have a Gondwanaland origin but represent relict elements of families with northern (Laurasian) distribution patterns. In southern Africa the Oopeltinae (a group of endemic slugs) are a subfamily of the Holarctic

¹ Paper read at the Symposium on the biology and evolution of Mollusca, Sydney, 21-25 May 1979.

Arionidae and the genus *Fauxulus* (— perhaps also *Afriboysidia*) belongs to the Palaearctic family Orculidae. These are palaeogenic elements irrelevant to the topics discussed here (vide Van Bruggen, 1969: 101, 1978: 896).

The terrestrial molluscs of the Ethiopian or Afrotropical and Australian Regions have comparatively little in common. Apart from a limited number of cosmopolitan or near-cosmopolitan families and some circumtropical or near-circumtropical groups, there are two Gondwanaland families. The first category, the near-cosmopolitan families, consists of groups such as the Pupillidae *sensu lato*, the Valloniidae and Succineidae, the latter two only sparsely represented in both regions. The second category, the near-circumtropical families, encompasses groups such as the Subulinidae (sparsely represented in Australia, but very diverse in Africa and elsewhere). The two Gondwanaland families are the Rhytididae or Paryphantidae, and the Charopidae (Sølem, 1976, 1978), formerly part of the large complex called Endodontidae (see, e.g., Zilch, 1959) and in that context cosmopolitan.

As regards Gondwanaland — families, the Ethiopian Region harbours five families of terrestrial pulmonates that may be regarded as belonging to this category, the Aperidae, Dorcasiidae, Corillidae, Charopidae, and Rhytididae (Van Bruggen, 1977, 1978). All occur in southern Africa in a wider sense; table 1 shows their status in Africa, their possible relationships in the form of surmised sister groups and the distribution of these. The Aperidae are small to fairly large (ca. 25-120mm when alive) carnivorous slugs; the sister group may be the family Rhytididae. Incidentally, the range of the Aperidae more or less coincides with that of the African Rhytididae (Van Bruggen, 1978, figs. 8 and 7a). The

family	status in Africa (all southern Africa s.l.)	sister groups and its distribution
Aperidae	endemic family, 1 genus (<i>Apera</i>) with 12 species	? Rhytididae: South Africa, Seychelles, New Guinea and as far west as Borneo, Australia, New Caledonia, New Zealand, SW Pacific Islands
Dorcasiidae	endemic family, 3 genera with 1 species (<i>Tulbaghinia</i>), 4 species (<i>Dorcasia</i>), and 10 species (<i>Trigonephrus</i>) respectively	Strophocheilidae (+ Megalobulimidae): South America
Corillidae	1 endemic genus (<i>Sculptaria</i>) with 16 species	Corillidae of southern Asia
Charopidae	probably ca. 20 endemic genera with ca. 120 species	other Charopidae elsewhere
Rhytididae	2 endemic genera with 5 species Rhytididae (<i>Nata</i>) and 17 species (<i>Natalina</i>) respectively	Australian + New Zealand

TABLE 1. African (i.e., Ethiopian Region) pulmonate Gondwanaland families.

Dorcasiidae, another endemic family with a slightly more diverse pattern (Van Bruggen, 1977, fig. 1; 1978, fig. 6), have fairly large to large shells (8.0-39.5 x 15.0-45.0mm) and are desert and semidesert snails (with one exception in the mountains of the south western Cape Province). The giants of South America, the Strophocheilidae with the recently separated Megalobulimidae (Leme, 1973), are most likely to be the vicariant sister group of the Dorcasiidae (cf. Sølem, 1978:91). The Corillidae in Africa consist of a single genus, *Sculptaria*, with a fair diversity as regards species, which are all small (major diameter of

shell 5-10mm) desert and semidesert dwellers (Van Bruggen, 1978, fig. 4). The sister group of these most probably is the remaining part of the family which shows a more or less continuous vicariant distribution in southern Asia. Among the African Gondwanaland pulmonates the Charopidae show the greatest diversity. The taxonomy of the ca. 120 known species (Connolly, 1939; Van Bruggen & Verdcourt, 1965; Solem, 1970; Sirgel, 1980), all smallish to very small indeed (major diameter of shell 1.2-23.3mm), has not been sufficiently worked out, except for one genus endemic to southern Africa, *Afrodonta*, with eleven species (Solem, 1970). At the moment almost all other species are classified with the genus *Trachycystis*, of which ca. twenty subgenera and subgeneric units are distinguished. Subgeneric units are as yet unnamed taxa probably of subgeneric rank. It is quite likely that these may be raised to generic rank when properly revised. In the mollusc fauna of southern Africa the Charopidae form a dominant element (Van Bruggen, 1978, fig. 1, for

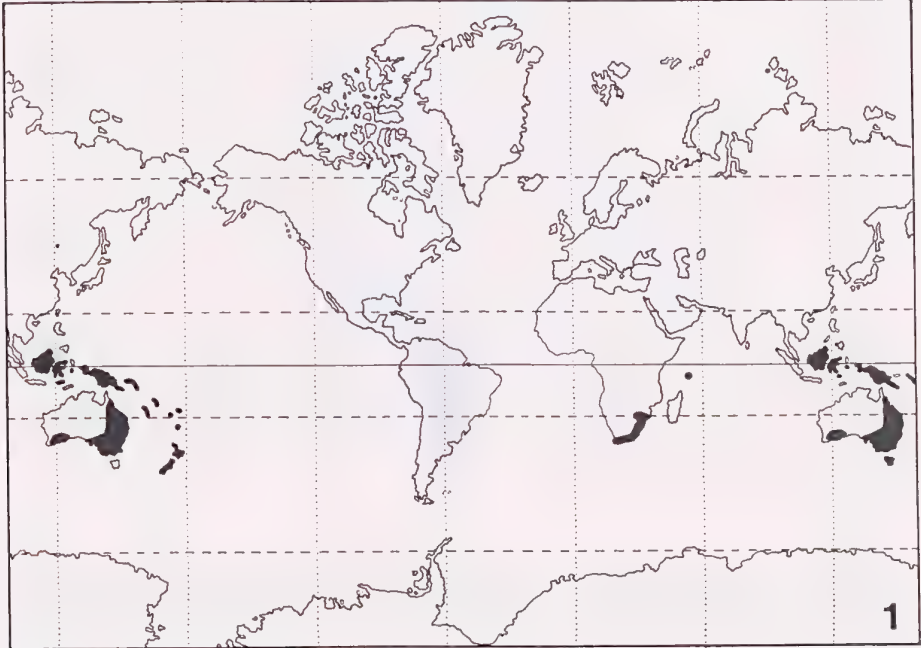


FIGURE 1. World distribution of the pulmonate family Rhytididae (Paryphantidae); note isolated occurrence on Seychelles Islands north of Madagascar.

RHYTIDIDAE (= Paryphantidae)

data after Connolly, 1939 (southern Africa, with corrections)
Burch, 1976 (Australia)
Powell, 1976 (New Zealand)

area	total Pulmonata species genera		Rhytididae genera % of total		Rhytididae species % of total	
Southern Africa	635	69	2	3%	22	3%
Australia	707	188	13	7%	42	6%
New Zealand	294	44	5	11%	35	12%

(some data approximate)

TABLE 2. Local diversity of the pulmonate family Rhytididae (Paryphantidae) in Africa, Australia and New Zealand.

Endodontidae substitute Charopidae, because in Solem's new taxonomy almost all species will be classified with that family except for a few Punctidae). Dominant families, loosely defined, are families that by virtue of their local diversity make up a significant segment of the total number of species, e.g., Camaenidae in Australia and Helicidae around the Mediterranean. It is well-nigh impossible to guess what the sister group of the African Charopidae is; the family as a whole is very widely distributed in the southern hemisphere and at the same time shows a remarkable diversity in the Australian Region *sensu lato*.

Finally, the Rhytididae are in Africa represented by two endemic genera with a total of 22 species (Van Bruggen, 1978), carnivores varying in size from very small to very large (major diameter of shell 4.5-75.5mm). The two southern African genera form a compact group; possibly the Australian and New Zealand Rhytididae together form the vicariant sister group of the African Rhytididae, which leaves the problem of the few taxa on the western Indian Ocean island group of the Seychelles (genus *Priodiscus*). The African distribution of the family (Van Bruggen, 1978, fig. 7a) shows that the two genera only occupy the humid southeastern parts of the continent on and east of the escarpment. The world distribution of the family (fig. 1; see also Solem, 1979, fig. 4) shows a typical Gondwanaland pattern, although the group is not represented in either Madagascar or South America (bicontinental pattern). The Rhytididae have penetrated far northwest, as far as Borneo, thus beyond Wallace's line. At present the greatest diversity of the family is in the Australian Region (table 2). This table features the comparative role of the Rhytididae on the main land areas Africa, Australia and New Zealand. Attention should be drawn to the increasing importance of the family from west to east. In southern Africa the Rhytididae are a numerically comparatively very insignificant group with only 3% of the genera and of the species. In Australia the family is roughly twice as important, whatever these figures stand for. However, in New Zealand the Rhytididae are a dominant family with 11% of the genera and ca. 12% of all pulmonate species, or double the figures for Australia which implies four times those for Africa. Outside these large land areas the Rhytididae are found on a host of larger and smaller islands, although to my knowledge never in such a dominant position. In New Guinea, for example, there are only two non-endemic genera and a total of only six species (Van Benthem Jutting, 1964). This is perhaps a naturally impoverished number of taxa, a low diversity near the northernmost limits of the distribution.

Rhytididae are powerful carnivores, feeding on what is somewhat indifferently called 'soft invertebrates', mainly other snails "such as achatinids and subulinids and possibly any other snail sufficiently common to fall victim to these predators' (Van Bruggen & Appelton, 1977: 33). In Africa various groups of snails seemingly compete for the same niches, viz., carnivorous slugs of the family Aperiidae (largely sympatric with the Rhytididae), and the very diverse, almost circumtropical family of the Streptaxidae. Members of the latter family are generally small to very small (shell length 1.5-21.5mm) where they are sympatric with the Rhytididae, although species of about equal size are known to occur together. The real giants among the streptaxids (*Edentulina*, shell up to ca. 50mm long) occur in Central Africa and in Madagascar where there are no Rhytididae. No information is available as regards carnivorous snails seemingly competing with the Rhytididae outside Africa, except for the Seychelles Islands where the few small and insignificant rhytidids are sympatric with a fairly diverse assemblage of streptaxids (Mahe: 1 *Priodiscus* and 13 Streptaxidae; Praslin: 1 *Priodiscus* and 3 Streptaxidae; Silhouette: 2 *Priodiscus* and 7 Streptaxidae; data from Sykes, 1909).

The second Gondwanaland pulmonate family shared by Africa and Australia is the Charopidae. The state of the taxonomy of the family in Africa does not allow one to extensively dwell upon this group. Fig. 2 shows the world distribution of the family with data from outside Africa mainly derived from a number of papers by Solem and additional information supplied by this author (in litt., 1979); although almost completely limited to the southern hemisphere the range appears to be considerable. The distribution in Africa covers a limited area in southeastern Africa with headquarters in Natal, while petering out quickly north of the Zambezi River with a few species reaching the equator in Kenya. As

yet there are no exact figures available for comparing the known diversity in Africa with that elsewhere; the few data are set out in table 3. All numerical data exclude newly discovered but as yet unpublished species. According to Dr. Solem (in litt., 1979) Burch (1976 : 132-133 s.n. Punctidae) enumerates 30 genera with a total of 109 species considered Charopidae by the former, viz. Burch's Endodontinae (pp. 132-133 minus *Theskelomensor*) and Phenacohelicinae (p. 133). The data for Africa and Australia show generic diversity in the Charopidae in Australia yet to be less than in Africa, while data on the species level do not seem to differ significantly. The position in New Zealand, the southwest Pacific islands and elsewhere is utterly different. According to Dr. Solem (in litt., 1979) Powell (1976: 115-119) enumerates 19 genera with a total of 145 species considered Charopidae by the former, viz. Powell's Endodontidae (pp. 115-116), Flammulininae (pp. 116-118) and Otoconchinae (p. 119). The malacofauna of New Zealand shows a marked

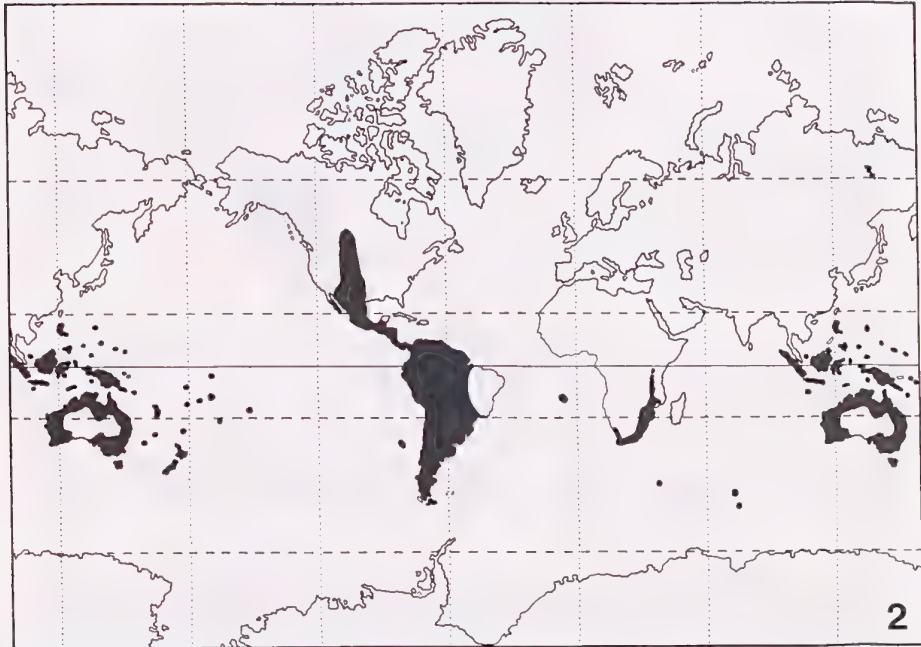


FIGURE 2. World distribution of the pulmonate family Charopidae (Endodontacea); note isolated occurrence on many islands groups, e.g., subantarctic islands, St. Helena Island (Atlantic Ocean), Juan Fernandez Island (W. of South America). Main data supplied by Dr. A. Solem (Chicago).

CHAROPIDAE (= Endodontidae Zilch p.p.)

data after Connolly, 1939 (southern Africa, with corrections)
Burch, 1976 (Australia, interpretation by Dr. A. Solem)
Powell, 1976 (New Zealand, interpretation by Dr. A. Solem)

area	total Pulmonata species genera		Charpidae genera % of total		Charopidae species % of total	
Southern Africa	635	69	ca. 20	ca. 29%	ca. 120	ca. 19%
Australia	707	188	30	16%	109	15%
New Zealand	294	44	19	43%	145	49%

(some data approximate)

TABLE 3. Local diversity of the pulmonate family Charopidae (Endodontacea) in Africa, Australia and New Zealand.

preponderance of Gondwanaland elements; apart from the Rhytididae and Charopidae most of the other endodontoids and the Bulimulidae and Athoracophoridae (and some other families as well) also belong to this assemblage of taxa.

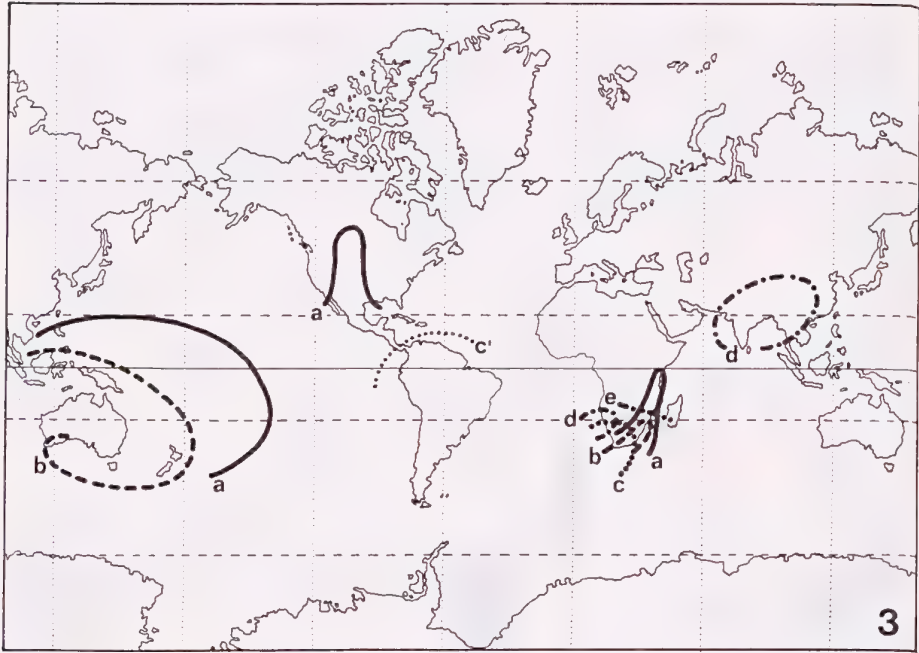


FIGURE 3. Northern limits of Gondwanaland families in Africa and elsewhere; a = Charopidae, b = Rhytididae, c = Dorcasiidae, c' = Strophocheilidae and Megalobulimidae (surmised sister group of Dorcasiidae), d = Corillidae, e = Aperidae.

family	in Africa	in Australasia	elsewhere
Rhytididae	ca. 23° (Transvaal)	ca. 0° (Equator)	ca. 4°30'S (Seychelles)
Aperidae	ca. 19°S (Rhodesia)	—	—
Dorcasiidae	ca. 19°S (South West Africa)	—	sister groups as far north as ca. 11°N (Trinidad and Tobago)
Corillidae	ca. 16°30'S (border of Angola and South West Africa)	ca. 30°N (Tibet)	—
Charopidae	ca. 0° (Equator, Kenya)	ca. 20°N (Marianas and Philippines)	ca. 16°S (St. Helena) ca. 43°N (Idaho, U.S.A.)

TABLE 4. Northernmost limits of the distribution of African pulmonate Gondwanaland families.

Finally attention is drawn to a peculiar phenomenon of the distribution of the Gondwanaland families in Africa: why have these groups in Africa never penetrated as far north as the same families or their (surmised) sister groups have done elsewhere? And why is the diversity of these families so comparatively low in Africa? Table 4 and fig. 3 indicate the northern limits of the various Gondwanaland families discussed here. The map shows that all Gondwanaland families occur well north of the equator outside Africa, while in

Africa only the Charopidae reach the equator. The map also shows the limited area in Africa occupied by the Gondwanaland families. The diversity of these groups has been shown in table 1 and amounts to a total of only five families, ca. 27 genera and ca. 185 species for the whole continent. The evolutionary success of these groups as measured by diversity and area occupied is thus shown to be comparatively very limited.

There may be an explanation for this in the history of Africa through time. Africa has enjoyed an insular existence since losing contact with South America in the Middle Cretaceous, ca. 105 million years B.P., while the connections with Antarctica were already severed in the Upper Jura — both Australia and New Zealand were still connected to Antarctica at the time Africa was already an island. The last link with Antarctica to be cut was that with South America, sometime in the Cretaceous. Africa floated northward and finally collided with the remains of Laurasia, thereby linking up with Europe and Asia. During the Miocene a great and almost continuous forest belt covered large parts of both Asia and Africa, resulting in many forest elements shared by both regions. The following hypothesis may now be considered. After the establishment of the above connection the many and varied land molluscs of Laurasia vigorously started to penetrate Africa, meeting and competing with the Gondwanaland elements already locally present or dispersing northward. By sheer numerical force of the northern elements, as reflected by their present-day diversity, the Gondwanaland families remained restricted in their expansion and distribution. Poor land connections to the north prevented an invasion on a similar scale in the Australian Region, reason why the Gondwanaland families proliferated in that part of the southern hemisphere. The position in America is somewhat different because of the repeated interruption of the connection between North and South America.

Attention should be drawn to the fact that none of the African Gondwanaland families occurs on Madagascar. This island does harbour southern land snail families, but these have distribution patterns that do not include Africa. Madagascar appears to have lost contact with the African continent at a comparatively early stage and has been an island ever since, which may partly account for this phenomenon (see e.g., maps in Cox, 1974).

The above-discussed hypothesis attempting to explain the poor success of the African Gondwanaland snails is seemingly supported by some general data on various groups of invertebrates in Werger's treatise (1978); however, this topic has not been worked out in detail.

An attempt to find support in distribution patterns of plants met with great response from Dr. M.M.J. van Balgooy (Leiden), who supplied maps of four families of Gondwanaland angiosperms: Cunoniaceae, Monimiaceae, Myoporaceae, and Proteaceae. All show tricontinental Gondwanaland distributions and a comparatively low diversity in Africa, and all reach their northern limits outside Africa considerably further north than in Africa. The Proteaceae penetrate far north in Africa, but still reach noticeably higher latitudes in both Asia and Africa. These distribution patterns seemingly confirm the above malacological data and thus may have found their origins in the same causative phenomena.

Climatic factors must have had their own influence. Tropical Tertiary climates may have contributed in driving the temperature Gondwanaland elements southward so that these became concentrated at the southern tips of the southern continents (see e.g., Horton, 1974). This certainly does not seem to apply to the terrestrial molluscs here discussed, unless these subsequently adapted themselves to tropical conditions and moved northward in the areas outside Africa. Rhytididae — Charopidae both occur under fully tropical conditions in e.g. southeast Asia, and the Charopidae are also found in tropical America. This, of course, leaves us with the problem: why did these families become restricted in southern Africa and not elsewhere in the southern continents?

Acknowledgements are due to Dr. A. Solem (Field Museum of Natural History, Chicago) for kindly evaluating existing lists of Gondwanaland Endodontacea and supplying distribution data of Charopidae, and Dr. M.M.J. van Balgooy (Rijksherbarium, Leiden), for supplying botanical data.

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SYMPOSIUM ON THE BIOLOGY AND EVOLUTION OF MOLLUSCA

A Symposium on molluscs was held in The Australian Museum from the 21st to the 25th May, 1979. It was organised by Dr. W.F. Ponder of The Australian Museum and Dr. A.J. Underwood of the University of Sydney with the assistance of the other members of The Australian Museum's Department of Malacology and TAMS volunteers, and students from the University of Sydney. Over 140 delegates attended the Symposium representing 10 countries and 47 papers and 26 posters were presented. The abstracts of the papers and posters are published in this issue of the Journal.

It was agreed by all that participated that the Symposium was an extremely worthwhile and successful event, not only in providing a forum for presenting information and for meeting people with similar interests but, particularly, in enabling scientists and students to gain a broader knowledge and appreciation of the Phylum containing the animals on which they have chosen to work.

Mollusca: the first hundred million years

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Molluscs appear to have evolved from free-living spiculose flatworms in the latest Precambrian (middle Vendian) between 650 and 600 million years ago. The oldest fossil molluscs are found in earliest Cambrian (early Tommotian) deposits of Siberia and China and are about 570 million years old. These diverse faunas show that 4 classes (Aplacophora, Monoplacophora, Gastropoda and Rostroconchia), 8 orders, and about 9 families of molluscs had appeared before the beginning of the Cambrian. The Precambrian molluscs were probably very small (~1mm in size) and hence are inconspicuous as fossils.

Cambrian molluscs are not common fossils but important taxa have been described from the Early Cambrian of Siberia, China, western Europe and Massachusetts; the Middle Cambrian of Australia, Korea, Czechoslovakia and Canada; and the Late Cambrian of Antarctica, Australia, China and the United States. By contrast, Ordovician molluscs are common and widespread. These data suggest that: 1, at least 7 of the 8 classes of molluscs evolved prior to or during the Cambrian (570-500 million years ago); 2, the diversity of molluscs measured in terms of the numbers of orders and families present remained low (about 10 orders and 10 families) until the beginning of the Late Cambrian about 520 million years ago; and 3, an exponential increase in the diversity of molluscs commenced about 520 million years ago and lasted for about 40 million years until the end of the Early Ordovician. By the later Ordovician molluscan diversity had stabilised at 8 classes, 17 subclasses, about 30 orders and about 70 families.

Comparative studies of the skeletal anatomy (and inferred functional and soft-part morphology) of Cambrian and Ordovician molluscs suggest that the diversification of the phylum occurred in the following ways (dates in square brackets):

- 1, *Neopilina* - like limpet-shaped monoplacophorans (Scenellidae) evolved from chiton-shaped spiculose aplacophorans [Vendian].
- 2, animals with a taller curved shell, fewer pairs of gills, and fewer pedal muscle insertions (Helcionellidae) evolved from the Scenellidae [Vendian].
- 3, lateral narrowing of the helcionellid shell produced first the Stenothecidae [Vendian] and then ribeiriid rostroconchs [Vendian]. In these forms the shell-attached pedal muscles were enlarged anteriorly and posteriorly and reduced laterally.
- 4, the development of a flexible dorsal shell margin in primitive rostroconchs resulted in the evolution of the Bivalvia from the Rostroconchia [Early Cambrian]. The anterior and posterior pedal muscles of primitive rostroconchs were divided between left

and right valves in the Bivalvia. 6, asymmetric coiling of the descendants of some helcionellid monoplacophorans (Pelagiellidae, initiated torsion and the origin of the Gastropoda [Vendian]. Torsion occurred after one of the original pair of lateral shell-attached pedal muscles had been lost [Vendian]. 7, planispirally coiled bellerophon Monoplacophora evolved from helcionellid Monoplacophora [Middle Cambrian]. In tightly coiled forms the shell-inserted pedal muscles are reduced to a single pair. 8, elevation of the intake-tube of snorkel-bearing monoplacophorans (Yochelcionellidae) produced a tall, backward-curving shell [Middle Cambrian]. The first cephalopods may have evolved from septate descendants of the Yochelcionellidae by modifying the tissues of the snorkel to form a primitive siphuncle [Late Cambrian]. 9, enlargement of seven or eight dorsal spicules of a primitive aplacophoran produced the first chiton (*Matthevia*) [Late Cambrian]. Its series of dorsal spikes is homologous with the eight imbricate plates of younger polyplacophorans. 10, the better designed bivalves replaced more primitive rostroconchs [Middle Ordovician]. 11, cephalopods succeeded the Monoplacophora as the most diverse molluscan class [Ordovician].

Origin and relationships of the Mollusca

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Up to now, the question of molluscan origin has not been answered. As possible pathways of the lineage are discussed: the derivation of the molluscs from annelids or platyhelminthes as well as the combined evolution of molluscs and annelids from aschelminthes or larval stages of coelenterates. Also, the relationships between the classes of the Mollusca are not clear.

The classical arguments for the different interpretations are collated. Moreover, some new findings from paleontology, comparative anatomy, ultrahistology, and biochemistry are taken into consideration. Fossil species from the transition field between ancestors and molluscs are not known, and the possibility to find connecting links is minute. Therefore, the clearing up of the relations may be achieved only in recent species within the limits of circumstantial evidence. Particular stress is laid upon the valuation of the fine structure of specialized tissues and organs. Especially, the situation in flatworms, annelids and molluscs is considered. According to the method of Hennig, it is tried to evaluate the compiled characteristics as plesiomorphisms or apomorphisms and to collate them into a diagram of argumentation, following Hennig. This diagram reflects the probable interrelationships of the molluscan classes as well as the relationships to other phyla.

New Zealand Middle Cambrian Mollusca: their nature and bearing on early molluscan evolution

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Recent palaeontological research has shed new light on the identity of a number of the earliest molluscs that existed during the Cambrian Period, some 500 to 570 million years before present. This upsurge of interest in Cambrian molluscs has provided the impetus for a restudy of a variety of minute fossils that were known to occur in several New Zealand limestones of late Middle Cambrian age (about 520 million years before present).

The fossils occur as phosphatic moulds. By dissolving fragments of limestone in dilute acetic acid the fossils are readily recovered as part of the insoluble residue. Although internal moulds are most common, some fragments exhibiting external ornamentation are found occasionally. By comparison with modern day molluscs, Cambrian forms are of small size, and as none of the New Zealand forms have a maximum dimension of much more than two millimeters, they are of a size appropriate for examination by scanning electron microscope.

Despite the preservation of appreciable detail it is difficult to assign most forms to recognised higher taxonomic categories due to lack of diagnostic skeletal characters, such as muscle scars. The most commonly occurring fossil is the enigmatic *Pelagiella*, generally regarded as a mollusc and of world-wide distribution in Cambrian rocks. In addition to *Pelagiella*, genera known also from Australian Middle Cambrian strata include *Protowenella*, *Latouchella* and *Mellopegma*.

Of interest are two hitherto undescribed univalves, one showing strong lateral compression like *Mellopegma*, the other much less so, whose internal cavities are transversely partitioned by a plate resembling the pegma of younger riberioid rostroconchs. *Heraultipegma*, from the late Cambrian of France, has been regarded by some authors as the earliest rostroconch by virtue of the presence of a small pegma. A re-examination of additional material from the type locality reveals no consistent morphological feature that can be regarded unequivocally as a pegma of the sort possessed by riberioid rostroconchs. If *Heraultipegma* is therefore excluded from the Class Rostroconchia there remain no known fossils older than the New Zealand forms with characteristic rostroconch morphology. *Heraultipegma*, though not regarded as a rostroconch, is still considered to be an unusual kind of mollusc because of its distinctive morphology including a highly acicular skeletal fabric that is compatible with molluscan affinity (but not Arthropoda).

Also present are specimens of a tall-coned, moderately compressed univalve that is assigned to the Family Hypseloconidae. Although the overall shape of this form is reminiscent of early Plectronocerida (Cephalopoda) the absence of septation plus siphuncle precludes any close phylogenetic link between the two. Nevertheless, such an elongate form seems a plausible precephalopod ancestor occurring as it does in rocks only slightly older than the *Knightoconus* — bearing strata of Antarctica and perhaps 10 or 15 million years older than rocks containing the earliest known cephalopod, *Plectronoceras*.

Of particular interest are specimens of a bivalve with well developed dentition. Along the prominent hinge line there are four or five short, oblique bar-like teeth, both back and front, which converge ventrally toward the middle of the shell interior. An edentulous segment, located medially, may indicate a site of ligament attachment. On the basis of shell form and dentition this fossil is regarded as the earliest known representative of the subclass Palaeotaxodonta.

Filter feeding aspidobranch limpets from submarine thermal springs of the Galapagos Rift — A new superfamily of archaic archaeogastropods

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Numerous specimens of a new limpet were collected in early 1977 near vents of submarine thermal springs at a depth of 2,450m on the Galapagos Rift using the deep

submersible vessel ALVIN. They are conspicuous members of a previously unknown community of filter feeding animals that consume chemosynthetic sulphur-oxidizing bacteria.

The cap-shaped shell is composed of lamellar aragonite, has an irregular circular aperture with a maximum diameter of about 30mm, sculpture of fine radial ribs, and a fibrous periostracum that overhangs the edge. The protoconch is small, unsculptured; the first teleoconch whorl is smooth, has a deep suture and a prosocline lip; the next whorl is uncoiled. The shell muscle (and muscle scar) is relatively small, crescent-shaped, posterior to the apex, opening toward the left, enveloping the viscera but not the deep mantle cavity that extends along the entire left side. A low shell ridge originates on the columellar region of the early coiled phase and extends through 1/4 the arc of the muscle scar.

The neck of the animal is long, broad and deeply grooved along the left side. Eyes are lacking; cephalic tentacles are directed posteriorly. In males of all sizes the left tentacle, which lies in the inhalent side of the mantle cavity, is larger than the right. The foot has an anterior pedal mucous gland and a series of epipodial tentacles along the posterior and right posterior sides.

The single bipectinate gill is massive and is attached only on the ventral, efferent side; long filaments overhang the neck and reach a food groove on the dorsal right side of the neck. The food groove cuts diagonally toward the mouth, over the cephalic tentacle, not under it as in pectinibranch filter feeders. The feeding mechanism is evidently similar to, and convergent with, that of the mesogastropod family Calyptraeidae.

The radula is rhipidoglossate and is unlike any other known. Salivary glands are lacking; the intestine has a long anterior loop; the anus is directly over the neck. The gonad connects to the right kidney; in females the opening to the mantle cavity has a rosette-shaped lip, which is lacking in the males. None of the organs have the paired condition of zygobranch archaeogastropods. Unlike zygobranchs and trochaceans the heart is monotocardian and the rectum does not penetrate the ventricle. Efferent branchial and pallial veins enter the auricle at its posterior end.

A truly bipectinate ctenidium specialized for filter feeding has heretofore been unknown and considered unlikely. Paleontologists, however, have speculated that some extinct archeogastropods had to be filter feeders because the shells were too massive for the animal to be mobile. This new limpet demonstrates how a bipectinate ctenidium may be modified for filter feeding: filaments are lengthened and increased in number, afferent support is lost, and complete efferent attachment is necessary. The early coiled phase suggests that it is derived from coiled predecessors. I surmise that its affinity is with extinct groups in which the gill structure was very likely similar. In the classification of Knight and others (1960) it is placed in a new superfamily provisionally assigned to order Archaeogastropoda, suborder Macluritina.

The evolution of some higher taxa in gastropods

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Comments are confined to the possible evolution of gastropods from a procerithiacean stock which may represent a single line of descent from archaeogastropods and appears distinct from the *Littorina-Rissoa* taxa. The evolution of the procerithiaceans may have been related to the success of a high-spired gastropod living on a soft substratum, the habitat of Recent descendants. The superfamily Cerithiacea, pruned of families known to

have been placed there erroneously, is considered to include some of the most primitive living representatives. To these are related the strombids which have developed a remarkably extensile snout for probing soft substrata. This is followed by the development of the acrembolic proboscis capable of complete retraction and associated with flesh eating. It occurs in the sponge-feeders, triferids and cerithiopsids which retain the *Cerithium*-like shell, and the coelenterate feeders, mathildids, epitoniids and architectonicids in which prosobranch characters outweigh opisthobranch ones, and on this basis they are retained in the caenogastropods and not regarded as opisthobranch. The balance towards opisthobranchs is turned in pyramidellids in which the acrembolic proboscis is used for piercing and sucking animal tissues. No other evolutionary line of procaenogastropods has evolved a mosaic of opisthobranch-prosobranch characters and this is the main basis for suggesting that opisthobranchs have arisen from the procerithiaceans. It is proposed to subdivide the subclass Opisthobranchia into two superorders, the Pyramidellimorpha and Euopisthobranchomorpha, the origin of the pulmonates being close to the latter. We know of other gastropods which on the basis of certain characters must have had an origin close to that of the Euopisthobranchomorpha, these are the Omalogyridae and Rissoellidae which should undoubtedly be removed from the Rissoacea and raised to superfamily level.

The heterogastropods are not considered to be a valid group of gastropods, but a convenient descriptive term for those which may have followed some initial steps towards the opisthobranch grade.

Scar tactics of gastropods: predation and the fossil record

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Predation by means of crushing is an important cause of death for many gastropods, especially in shallow-water tropical environments. The increasing incidence of characters conferring resistance to crushing (strong sculpture, apertural teeth, slit-like apertures, etc.) since the middle Mesozoic suggests that the intensity of crushing has increased over the past 150 to 200 million years. In order to evaluate this hypothesis, the incidence of repair-marks on shells has been examined in fossil and Recent gastropods, and empirical relationships between the frequency of shell breakage in nature and incidence of shell repair are being derived. Preliminary data from Guam (Mariana Islands) and Majuro (Marshall Islands) suggest that there is a positive correlation between breakage and repair in at least three reef-flat gastropods (*Conus sponsalis*, *Rhinoclavis fasciata*, and *Strombus gibberulus*).

Reef-flat gastropods can be placed in three categories with respect to the incidence of repair. The first category contains species that have no significant escape in size from such crushing predators as crabs and fishes; repair in such species, which include small cerithiids, *Conus sponsalis*, and *Strombus gibberulus*, is rare. The second group of species is characterized by frequent shell repair; they have a distinct escape in size from crushing predators, but the structure of the lip is such that an attacker usually succeeds in chipping away part of the body whorl, so that the snail, must repair the injury. Examples include the larger cones, most species of *Rhinoclavis*, and all terebrids. The third category of species contains those with a strongly thickened lip which is rarely breached by an attacker once the gastropod has achieved a sufficiently large size; examples may include *Strombus mutabilis*, *Cerithium nodulosum*, and *Bursa bufonia*.

Food specialisation and the evolution of predatory gastropods

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Predatory prosobranch gastropods are an extremely diverse trophic group including some 26 families of meso- and neogastropods. A wide variety of prey types are consumed by the gastropods including most groups of larger invertebrates, and an array of specialised techniques has been evolved in order to catch, immobilise and extract the prey. Evidence is presented from studies of guilds of species in different tropical families that competition has been a major force in determining the food and habitat specialisations of the different predatory species. Similarly, over evolutionary time, competitive interactions may have resulted in the food and habitat specialisations of the different families. Most of the families of predatory gastropods appeared in a massive evolutionary radiation during the Late Cretaceous and evidence for the origin of the major groups will be reviewed. By comparison with living species the early predators from the Albian probably ate sedentary polychaetes and molluscs, whilst the more specialised families did not evolve until the Campanian and Maastrichtian stages. There was an exponential rise in the number of families and species until the Eocene, by which time it is probable that the main adaptive zones occupied by predatory gastropods had been largely filled. Evolution since then has consisted mainly of diversifications within the adaptive zones of particular families. The recent high diversity of food and habitat generalist species at high latitudes can be associated with the onset of polar cooling in the Late Miocene. The Turridae reached their present levels of high diversity during the Eocene and their relative importance at high latitude and in offshore habitats was established by the Lower Miocene.

Composition and origin of the molluscan fauna of the Tertiary of South Eastern Australia

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The Australian coastline has been divided into two regions based on the distribution of Mollusca and other marine invertebrates (Ekman, 1953; Wilson, 1971). These are the tropical Indo-Pacific faunal province and the Southern Australian faunal province. The latter has a unique temperate marine molluscan fauna with little in common with other regions and the molluscan fauna has for the most part its origin in the fauna of the Southeastern Australian Tertiary.

The Southeastern Australian Tertiary Mollusca fauna, part of which was first established in the Late Eocene, is composed, for the purposes of this discussion, of four elements (a) Australian — New Zealand, (b) Indo-Pacific, (c) Endemic and (d) Cosmopolitan. The proportions of the elements in the fauna fluctuated with time and during the Mid Tertiary the Indo-Pacific element was the largest because of an increase in migration of Indo-Pacific genera south when water temperatures rose. The Indo-Pacific element was much stronger in the western half of the South of the continent in the Eucla and St. Vincent Gulf

Basins from Early Miocene to Pliocene time and on the basis of this and other differences, two provinces have recognised in the Mid Late Tertiary, the Austral Indo-Pacific Province and the Southeastern Australian Province (Crespin, 1950; Ludbrook, 1969), the latter including the Murray, Otway, Bass and Gippsland Basins.

The fauna of the Southeastern Australian Province has been analysed in a manner similar to that done by Fleming (1967) for the New Zealand Tertiary, using similar criteria and the time ranges of 301 genera, thought to be representative of the fauna as a whole, have been plotted. Of these, 64 belong to the Australian-New Zealand element, 107 to the Indo-Pacific element, 86 to the Endemic element and 44 to the Cosmopolitan element.

Australian-New Zealand Element: Composed of genera common to Australia and New Zealand and not known to occur outside these regions. Fleming (1967) used the term Australian for this in his work. The proportion of the element in the fauna as a whole is about 29% in the Late Eocene, 32% in the Early Oligocene, then falling to 15% in the Pliocene and Pleistocene. In terms of actual numbers of genera present, there is a maximum of 49 in the Mid Miocene.

Indo-Pacific Element: The concept of this element is essentially that of Fleming (1967) and includes, in part, both the Present Indo-Pacific and Tethyan Eocene elements of handbook (1955). Examples of the later genera are *Orthochetus*, *Cypraedia*, *Ampullina*, *Sassia*, *Personella*, *Leptoscapa* and *Eocithera*.

The proportion of Indo-Pacific genera in the fauna as a whole is 25% in the Late Eocene, 21% in the Early Oligocene, rising to 34% in the Mid Miocene and remaining fairly constant in proportion (32%) through the Pliocene and Pleistocene. The maximum number of genera present is 76 in the Mid Miocene. Fleming's more thorough analysis gave about 100 genera in the Lower Miocene of New Zealand.

Southern Australian Endemic Element: This consists of genera not yet found outside the Southern Australian Region. In the Late Eocene it consisted of about 20% of the whole fauna but the proportion rises steadily with time to 36% in the Pliocene and Pleistocene. Absolute numbers are 20 in the Late Eocene, 68 in the Mid Miocene and 61 in the Pliocene and Pleistocene.

Cosmopolitan Element: These genera have a wide distribution through-out the world both in space and time. In the late Eocene they comprise about 27% of the fauna, drop to 14% in the Mid Miocene and rise to 17% in the Pliocene and Pleistocene. Absolute numbers of genera are, however, fairly uniform through the Tertiary at about 28 (22-32). Genera in this category are mostly bivalves.

The fluctuation of the proportions of the four biogeographic elements with time can be explained in terms of sea floor spreading and increase and decrease of sea water temperatures through the Tertiary. Following the splitting off of Australia from Antarctica in the Late Cretaceous, the Australian plate moved steadily northwards towards the tropics into the Indo-Pacific Realm. Increasing numbers of Indo-Pacific genera were therefore able to migrate into the Southern Australian region. In addition to the shift of the plate, sea water temperatures generally rose to a maximum in the Mid Tertiary, thereby allowing many Indo-Pacific genera to penetrate south. These genera gradually died out as water temperatures dropped. The greatest generic diversity is in the Mid Miocene when the effects of both the northward drift and increase in water temperatures were at their maximum.

In terms of proportions the Indo-Pacific and Endemic Elements have increased with time as the continent moved northwards at the expense of the Australian-New Zealand and Cosmopolitan Elements.

Functional interpretations of patterns in archaeogastropod radular morphology

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Morphological features of the complex rhipidoglossate radulae of marine archaeogastropods may be understood as consequences of interactions over evolutionary time of three major sets of constraints: phylogenetic, ecological and mechanical. Basic phylogenetic patterns have been identified in taxonomic research as constellations of associated characters that are conserved within families and genera. Ecological factors (notably substrate types and food sources) have led to specializations that have been superimposed repeatedly on basic phylogenetic patterns across the order. Scaling relationships and correlations between tooth dimensions and particle dimensions in deposits, on grazing surfaces, and in gut contents constitute strong implications, if not unequivocal demonstration, of ecologically superimposed adaptation.

Likewise, mechanical improvements that increase operating efficiency have been superimposed across the order, resulting in some striking examples of adaptive convergence. The basic movements of the odontophore and radula during feeding and the fundamental form of the rhipidoglossate radula form a conceptual biomechanical model that can be manipulated deductively to produce improvements in design. The predictive value of such analysis is confirmed by observations of actual configurations.

Six examples of mechanically significant patterns of adaptive convergence in rhipidoglossate radulae are discussed and illustrated in scanning electron micrographs and light micrographs. They are: (1) patterns of overlapping of tooth bases, shafts and cusps that transmit forces from one tooth to another; (2) patterns of interlocking elements within and between tooth rows to form joints that transmit forces in more complicated fashion, often involving a number of degrees of freedom; (3) losses of tooth shafts and blades coupled with modification of tooth bases to form specialized articulatory structures, particularly between the food-preparing and food-gathering portions of the radula; (4) structures related to load distribution on a single tooth, notably compressional ridges on the convex surfaces of tooth blades and those portions of tooth shafts where compressional forces are concentrated; (5) development of a pair of laterally situated, enlarged, primary food-preparing teeth per row in place of one centrally located primary food-preparing tooth; (6) development of radular asymmetry to accommodate enlarged food-preparing teeth when the radula is not in use and tightly folded.

Form, function and adaptive radiation in the Cerithiidae

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The family Cerithiidae comprises a large group of style-bearing prosobranchs in which sympatric genera and species are frequent. The family has undergone an elaborate adaptive radiation into various habitats. Adaptive peaks are seen in four major habitats: (1) subtidal

sand lagoons; (2) intertidal mud flats; (3) intertidal rubble flats; (4) high intertidal shores. The hypothesis is suggested that basic shell physiognomy, radular morphology, and anatomical features of the reproductive tract are directly correlated with substrate preference and trophic adaptation. The correlation of habitat with shell physiognomy can be demonstrated quantitatively.

Sexual strategies in Eulimidae (Prosobranchia)

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The family Eulimidae consists of a large number of species, most of which are parasites of echinoderms. They exhibit a very large variation in the way of parasitism and a still larger morphological variation, which is a result of their parasitic life. The most unmodified species retain all organ systems typical for mesogastropods, while some groups have lost almost all organ systems, except the reproductive organs and live as endoparasites. Some species live as ectoparasites only attached to their host by the proboscis and fall off as soon as the host is disturbed. Other species bury themselves in the body-wall of the host and/or form galls there. Some species live in the cloaca or in the coelomic cavity of the host.

I have met with the following sexual strategies in the family: (1) Gonochorists. (2) Protandric hermaphrodites. (3) Protandric hermaphrodites with environmental sex determination (ESD). (4) Simultaneous hermaphrodites (SH). (5) Specimens that start as females, turn to SH for a short time and then become females again. All species (except SH) exhibit a pronounced sexual dimorphism, with males of .1-7 times the height of the females. ESD seems to be common.

The occurrence of sexual dimorphism may have two reasons: (1) To make it possible for the female to take out more energy from the host and thereby also increase the number of offspring of the male. (2) Reduce the predation on the male. (1) might be the reason in some cases when the parasite is big compared with the host, e.g. some parasites of ophiuroids. (2) is probably more often the reason because (1) can be excluded in most cases as the parasites occur in large numbers.

Gonochorists occur only among genera that have a comparatively weak association with the host, often leave it and associate with a new host. This will give the parasite numerous occasions to meet other specimens for mating. Gonochorism probably originates from primarily protandric conditions, because the species that have the most unmodified morphology are all protandric hermaphrodites. Another evidence is that all related families (Aclididae and Epitonidae) also exhibit some hermaphroditical traits.

The protandric hermaphrodites change sex at a certain size or age, not influenced by environmental conditions. They have a weak association with their hosts, but their biology is too poorly known to allow comparisons with other strategies.

The following type of ESD has been found in Eulimidae: The first specimen that settles on the host becomes a female, later specimens males. This usually results in groups with one female and two or three males. Sometimes males changes sex to females, presumably as a result of the disappearance of the female. This strategy will ensure presence of both sexes and reduce predation on the male phase.

The advantage of SH is striking for some species which form permanent associations with their hosts, because they use only a minor part of the ovotestis for sperm production. Other SH have a restricted mobility on their host and spend upwards half their ovotestis on sperm production. In this case, as also in (5), the biology of the species involved is too poorly known to see the advantages of the sexual strategy.

Commensalism of the cap limpet, *Hipponix conicus*

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The cap limpet, *Hipponix conicus* lives only on the shells of other molluscs. The cap limpet is believed to obtain food from its host mollusc, but the nature of this association has not been examined thoroughly. Using field manipulative experiments, this study investigated the degree of dependence of the cap limpet on its host, the benefits for the cap limpet involved in the association, and the effect of the cap limpet on the host.

Factors Influencing The Distribution of *Conus* in east Australian waters

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The distribution patterns of shallow-water species of the gastropod genus *Conus* in East Australian waters are presented. These patterns were determined from the results of numerical analysis of locality records of specimens in both museum and private collections.

Within the latitude range of the study (15°S-35°S) three bands of high faunal similarity can be distinguished. Faunal discontinuities occur around 25°S and 31°S and delimit each faunal band. The existence of these faunal discontinuities, and hence the distinct faunal bands, can be explained in terms of variations in local topographic complexity and water temperature.

The *Conus* fauna of areas between 15°S and 25°S is composed entirely of species typical of the Indo-West Pacific faunal region. A band of faunal overlap, characterised by a decrease in the number of tropical species and an increase in the number of temperate water species, exists between 25°S and 31°S. South of 31°S only temperate species have been recorded. The faunal discontinuity which occurs around 25°S, separating the tropical zone from the overlap zone, is strongly related to the southern extreme of the Great Barrier Reef. South of this discontinuity local topographic complexity is reduced and does not favour large communities of *Conus*. The southern faunal discontinuity (31°S) is closely related to the northern limit of movement of the 20°C surface water isotherm.

Within the overlap zone the species composition of the tropical component of the community is dynamic and suggests that a large proportion of this species group are species which have migrated into the overlap area each year. The possibility of such migration is enhanced in most tropical species of *Conus* by the inclusion of a pelagic phase within their larval development. Water circulation patterns in the Coral and Tasman Seas are complex and consequently it is difficult to determine the origin of migrant species. Undoubtedly the Great Barrier Reef is the primary source of larvae for the overlap area however isolated species records for both *Conus* and other molluscan genera indicate that larvae may enter the East Australian Region from New Caledonia.

The northern limit of the distribution of temperate species is obscure and requires further study especially in the light of the different reproductive strategies employed by this species group.

Comparative Anatomy of *Bulinus* and *Isidorella*

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The Australian planorbid genus *Isidorella* Tate, 1896 has at various times been synonymised with the African genus *Bulinus* Muller, 1781 and as a consequence included, along with *Indoplanorbis* Annandale and Prashad, 1920 in the sub-family Bulininae. The diagnostic anatomical feature found exclusively in this sub-family is the ultrapenis which differs fundamentally from the normal planorbid copulatory organ.

Superficial examination of *Isidorella* and *Bulinus* indicates a degree of similarity belied by differences revealed in dissection. The salivary glands of *Bulinus* are tabular, passing through the circumoesophageal nerve ring and joining posteriorly. Those of *Isidorella* are flattened and branched where they lie on the buccal mass, and ribbon like where they pass through the nerve ring before joining. In *Bulinus* the insertion of the duct of the bursa copulatrix is on the proximal end of the vagina, whilst in *Isidorella* this duct is inserted at the distal end, almost at the female genital pore. The major difference is evident in the anatomy of the copulatory organ. *Isidorella* does not have an ultrapenis and consequently should not be placed in the Bulininae. Its copulatory organ is a normal pendant penis, though two distinct forms are found in different taxa within the genus. In *Isidorella sisurnia* from Western Australia and the Northern Territory the penis has a simple duct opening laterally with lobed processes distal to the pore. This structure is also found in larger animals from Western Australia and western New South Wales. The other form of penis, probably derived from that just described, has no duct running down its length, but opens out just distal to the entrance of the vas deferens into two longitudinally folded spatulate processes covered with a prominent ciliated epithelium. This structure is found in *Isidorella brazieri* from the east coast.

The small northern species *oppletora jukesii* has been synonymised with *Isidorella* and consequently included in the sub-family Bulininae. Dissection reveals that this species has a copulatory organ with a flagellum, the penis having a chitinated stylet. This structure is similar to the copulatory organ of *Physastra* and *Glyptophysa* and the affinities of *Oppletora* obviously lie here rather than with *Isidorella*.

The structure of the copulatory organ of *Isidorella* places the genus apart from all other planorbids, not only *Bulinus* and *Indoplanorbis*. The genus *Isidorella* should, therefore, be retained.

The distribution and biology of the freshwater gastropods *Physa* and *Physastra* in New Zealand

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Physastra (Planorbidae) and *Physa* (Physidae) are the only sinistrally coiled gastropod genera in New Zealand freshwaters. The former is represented by one, highly variable,

endemic species, *P. variabilis*, whereas at least one introduced species of *Physa* occurs. The commonest of these is almost certainly the European species *P. acuta*. *Physa* is widely distributed on both main islands of New Zealand in ditches, streams, lakes and ponds particularly close to urban areas and in agricultural areas or enriched water bodies. Its distribution resembles that of *P. (?) acuta* in South Africa where it has also been introduced recently. *P. variabilis* does not appear to be particularly common and occurs mainly in relatively undisturbed habitats including lakes and rivers. Comparisons with reliable distribution records from earlier this century indicate that *Physa* has replaced *P. variabilis* in many localities, for example in the rivers and streams around Christchurch. The two species are rarely found coexisting.

Growth and reproduction of both species has been studied in standardized laboratory conditions at water temperatures ranging from 6°C to 26°C. Growth rates of both species were similar (in terms of shell height increase) and snails attained similar maximum sizes. As has been found in other studies, snail density affected growth rate which was lower at higher densities. Fecundity of both species (eggs laid per unit time) also was similar but *Physa* reached reproductive maturity in half the time. The intrinsic rate of natural increase therefore is greater in *Physa* than *P. variabilis* and should enable it to build up large populations more rapidly.

In preliminary laboratory experiments, growth of *P. variabilis* was inhibited in the presence of *Physa* and all individuals died prematurely. However, when the species were kept apart by a nylon mesh screen which allowed free circulation of water, growth of *P. variabilis* was less inhibited and no snails died. This suggests that a form of interference competition occurred and further suggests that the geographic distribution of *P. variabilis* within New Zealand may have been reduced, at least in part, through competition with the competitively superior and more 'r-selected' *Physa*.

Freshwater gastropods of South Pacific Islands

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During 2 hydrobiological missions to South Pacific Islands in 1965 and 1971, the distribution of about 75 fresh — and brackish-water gastropods of different South Pacific Islands were studied (Southern East New Guinea and Long Island; New Britain, New Hebrides; New Caledonia; Fiji and Tahiti).

In the upper and middle courses in the mountains of the continental islands, species of Thiaridae such as *Melanoides* (*Melanoides*), *Thiara* in eastern New Guinea or the endemic species of *Melanopsis*, further the endemic species of Hydrobiidae, such as *Heterocyclus*, *Hemistomia* and *Fluviopupa* in New Caledonia are characteristic. The last genus is also represented in Fiji and other western South Pacific Islands. In stagnant waters or streams with slow current are typically species of the genus *Physastra* (in New Guinea are also *Amerianna*, in New Caledonia also *Glyptophysa*) in the western Pacific islands. The number of the typically "inland-species" is diminished eastwards to the oceanic islands. On the transition of the middle to the lower courses of the running waters start the occurrence of the species of Neritidae with the genera *Neritina* (*Neritina*) and *Septaria*. This family is represented mainly in the lower courses with many species of *Neritina* (*Neritina*) *N. (Vittina)*, *N. (Neripteron)*, *Clithon*, *Septaria* and *Neritilia*. They occur, like the species of the subgenus *Stenomelania* of *Melanoides* (with freeliving veligers!), till the brackish zones of the mouth regions. These regions are influenced by the recurrent flow of sea-water during

high tide. The Neritidae of these brackish areas are associated with typically brackish forms such as the genera *Paludinella*, *Assiminea*, *Truncatella*, *Cassidula* and *Pythia*. Sometimes also marine species such as *Littorina scabra* are sporadic to find. With the recurrent flow also exclusively marine groups, such as the opisthobranchs, with the species *Strubiella paradoxa* (Acochlidiacea) is immigrated till the freshwater zone of isolated islands.

A remarkable hydrobiid fauna from Lord Howe Island (Gastropoda : Hydrobiidae)

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The Hydrobiidae of Lord Howe Island consists of 5 genera and 9 species. Three species have subspeciated, one into five subspecies and two into two subspecies. The total number of species group taxa is 5, more than on the eastern Australian mainland. It is suggested that this fauna is the result of 3 separate colonisations during the Pliocene and/or Pleistocene. Most of the species live in small streams but one is adapted to living on waterfalls and another is subterranean in habit.

One introduction was from eastern Australia and this group (*Fluvidona* Iredale) contains 3 species and also appears to have given rise to 2 new genera, one of them becoming subterranean in habit. *Fluviopupa* Pilsbry, an introduction from the north, has developed into 2 species which live sympatrically in some localities. The remaining genus group, tentatively referred to *Potamopyrgus* Stimpson, contains only one species which is found living on waterfalls.

Problems of dispersal and speciation in this fauna were discussed.

Reproductive systems in the Athoracophoridae

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Considerable differences exist in the arrangement of reproductive organs in the Athoracophoridae. Species vary in the amount of coiling of the oviducal gland, in the relative length of the oviduct, in spermathecal position, and particularly in the degree of fusion between the male and female tracts. The basic pattern is exemplified by *Triboniophorus graeffei*, in which the male and female tracts separate on leaving the fertilisation pocket, the oviducal gland is incorporated in the wall of the oviduct, and the prostate gland is extended and lobular. In most New Zealand and subantarctic species a similar pattern is found, except that the oviducal gland is a distinct convoluted gland carried on one side of the oviduct, and the prostate is compact and discrete. In *Pseudaneitea ramsayi*, *Athoracophorus bitentaculatus* and *Palliopodex verrucosus* varying degrees of fusion of the male and female tracts are seen, with a diffuse prostate secreting at intervals into a male duct which forms a cleft in the wall of the female tract. It is considered that these three species evolved this condition independently.

Relationships within the family Rhytididae

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The Rhytididae is a large and complex family of carnivorous snails distributed from New Zealand and Australia, through the islands of the western Pacific with groups in the Seychelles and South Africa. The Australian fauna consists of about 27 species in 11 genera. These genera can be grouped with respect to shell, radula and anatomical characters into four or five groups. These can be compared with and notionally related to various non-Australian genera and groupings.

- Group I. *Victaphanta* — shell medium to large, almost smooth with almost no calcareous elements, umbilicus narrow to closed, radula of short, even lanceolate teeth, (40-60) — 1 — (40-60). Related to *Paryphanta*.
- Group II. *Prolesophanta*, *Saladelos*, *Echotrída*, *Tasmadelos* — shell small, smooth or with fine radial sculpture, radula of short, hook-shaped teeth to pegs, (14-26) — 1 — (14-26). Related to *Delos* and/or *Macrocyctoides*.
- Group III. *aphena*, *Strangesta*, *Namoitena*, *Occirhenea?* — shell small to large, with coarse, to fine radial sculpture and wide umbilicus, radula of grading lanceolate teeth, largest towards margin, (18-24) — 1 — (18-24). Related to *Ouagapia* and/or *Ptychorhytida*.
- Group IV. *Torresiropa* — shell small, carinate, radula not known. Possibly related to Group III.
- Group V. n. gen. for *capillacea* shell medium, wide umbilicus, sculpture of fine radial ribs, radulae with teeth grading to very large 9th or 10th tooth, (9-12) — 1 — (9-12). Related to *Rhytida* and possibly *Nata*.

Possible affinities of the genera in the family are discussed.

Patterns of Speciation in Camaenid Land Snails of the Kimberley, Western Australia

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Collections made by the author in the Pilbara and Kimberley areas of Western Australia in 1974, 1976, and 1977, together with materials in the Western Australian Museum, indicate a known fauna of about 150 species of camaenid land snails, two-thirds undescribed. Systematic revisions covering 75 species have been submitted to the Western Australian Museum for publication. These studies reveal that there are extensive alterations in the structures of both male and female terminal genitalia under conditions of congeneric sympatry. The terminal genitalia is used in species recognition by the snails. Also, there are quite different patterns of species distribution in several areas of the Kimberley. These differences suggest that speciation has occurred locally in different ways.

The Mitchell Plateau in the far northwest Kimberley is an elevated mound of bauxite bounded by big rivers and subject to a mean annual rainfall of 1,436mm (1968-1973), nearly all in November through March. It has a diverse representation of the camaenid land snail genus *Amplirhagada* Iredale, 1933 that show mosaic distribution patterns. Some species are restricted to the isolated islands of vine thickets, others tend to cluster among big boulders or talus in ravines, and one is widely distributed in the open eucalypt woodland. Species recognition is insured by major modifications in the male and/or female terminal genitalia. Aestivation site selection and strategy differ among species. Conchological similarities among species are many, but their ecology and anatomy differ dramatically.

The Napier Range inland from Derby is essentially a continuous high narrow limestone ridge running northwest to southeast that is periodically interrupted by either river gorges or strips of bare plains. Species of *Amplirhagada* show a leap-frog distribution, sometimes the shift occurring from one side of a gorge to the other, sometimes in as little as 100 meters of continuous and macroscopically uniform hillside. Some evidence of intergradation in a hybrid zone exists, and further fieldwork is planned in 1980 to study the contact zones between these closely related species.

The Ningbing Ranges, north of Kununurra and just west of the Northern Territory border, are broken up into short segments of narrow limestone ridges or a series of isolated limestone hills separated by alluvial plains and run almost directly north and south. Three genera are in linear replacement along the range, with the replacement areas not corresponding to major geographic gaps. Patterns of structural change under sympatry and local variation found in populations on neighboring hills indicate yet a third pattern of speciation in the Kimberley camaenids. The patterns of change outlined above are expected to be repeated in other groups of Kimberley camaenids and probably are applicable to Queensland and New South Wales camaenids.

A new order of interstitial, intertidal, systellommatophoran slug from Kaikoura, New Zealand based on a new genus and species (Mollusca : Systellommatophora)

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A new genus and species, the only known representative of a monotypic new systellommatophoran order is described. The new order is characterized by a stylommatophoran pulmonate type of reproductive system with male and female ducts opening via a common gonopore ventro-laterally on the right side behind the head, a posterior mantle cavity into which open the rectum, pneustome and a renal papilla and in having the anterior fifth of the foot modified into a sucker. The head lacks tentacles and eyes, but the notum is modified on each side of the head into a pair of weak lappets.

The species lives interstitially between MHWN tide and MHWS tide zones on a steeply-sloping shore composed of polished limestone pebbles 1-2cm in diameter, at Rhino Horns Point, Kaikoura Peninsula, South Island, New Zealand.

The superorder Systellommatophora is elevated to subclass level the implication being that Pulmonata and Systellommatophora are parallel derivations from different types of opisthobranch ancestors.

The function of certain organs in the Opisthobranch family Gastropteridae

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The Gastropteridae is a family of specialized cephalaspidean opisthobranchs in which the parapodia are greatly developed into swimming organs, though this action is not confirmed for all species. Three genera, 18 species and 1 subspecies are attributed to the family. The animals are, in most instances, characterized by a specific positioning of various appendages on the visceral hump or on the posterior edges of the parapodia. The function of the appendages has not been previously explained.

The Gastropteridae, like other lower opisthobranchs (Cephalaspidea, Anaspidea), copulate in a head-to-tail fashion, the animal in front assuming the receptive female role, that behind the aggressive male role. Some lower opisthobranchs (aglajids, aplysiids) are renowned for their long chains of copulating animals. Such chains are readily accomplished among aggregations of slow-moving bottom-crawling species. In the flighty Gastropteridae, where often the slightest stimulus causes the animals to swim, successful mating involves not only penial penetration but also the ability of one partner to clasp the other.

Anatomical studies indicate two basic types of male organ in the Gastropteridae. In *Gastropteron rubrum* and other large species of that genus, and in *Sagaminopteron ornatum*, the male organ comprises a short to long cylindrical penial papilla within its atrium and a very long winding prostate gland. During mating, the penial papilla is wholly everted. In small species of *Gastropteron* with a mamilliform projection on the posterior face of the visceral hump, such as *G. cf. fuscum* from north-eastern Australia, the male organ is relatively much smaller, comprising two parts, the larger the atrium, short penial papilla and short prostate gland, the smaller an accessory organ of spherical bulb connected by a slender duct to the atrium. During copulation, the atrium, penial papilla and accessory organ evert to form a bifurcate penial organ with the prostate gland contained within the everted atrium.

In *G. cf. fuscum*, successful mating takes place in the following manner. Animal A senses and approaches animal B directly from behind. A distends its mouth-parts and sucks in the posterior projection of the visceral hump of B, apparently stimulating B to reduce its crawling rate and assume a quiescent receptive attitude. A contracts forward and everts its male organ. The larger part (the penis proper) pushes forward between the right parapodium and the visceral hump of B to the genital aperture below the gill. The smaller part (the accessory organ) loops round and fastens to the outer face of the right parapodium by means of minute hooks projecting from its partly introverted bulb. With this three-way hold on B, A is wholly prepared for any sudden evasive action by its partner due to outside stimuli, probably even remaining attached during swimming.

Among the larger species, *G. cf. bicornutum* from north-eastern Australia and *Enotepteron flavum* from the Yellow Sea have a peculiar spherical appendage attached to the rear edge of each parapodium. These species probably each have a long cylindrical papilla. Theoretically, it would appear that during copulation, the penial papilla of animal A passes between the right-hand spherical appendage and the visceral hump of animal B, stimulating B to tumesce its spherical appendage and so hold the penial papilla in position. The right-hand spherical appendage in these species is seen as the homologue of the accessory organ of small species of *Gastropteron*. Bilateral symmetry accounts for the presence of the left-hand spherical appendage.

Symbiotic chloroplasts in sacoglossans from south-eastern Australia

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The existence of actively photosynthesizing chloroplasts, without the rest of the alga, in the digestive gland cells of a number of species of the order Sacoglossa is now well known. Studies of sacoglossans from New South Wales have shown that while members of the family Elysiidae can maintain active chloroplasts in their tissues, members of other families of the Sacoglossa may retain pigment from their food plants, or even damaged but recognizable chloroplasts, but that these associations are not capable of photosynthesis. It is proposed that camouflage provided the initial advantage to the animals of retaining plastids in their tissues for some time before digesting them, and that the exploitation of the ability of the chloroplasts to continue to photosynthesize was a later development in the evolution of the association. Since *Elysia* spp. can maintain actively photosynthesizing chloroplasts for periods of months, while chloroplasts isolated from plant tissues in the laboratory will only photosynthesize for hours or at best for a few days, it is clear that complex physiological adaptations are involved in the maintenance of the chloroplasts within the animal cells. Recent studies have concentrated on the inter-relationships between photosynthesis by the symbiotic chloroplasts and respiration by the mitochondria of the animal cells.

Predator or prey : nudibranchs and coelenterates

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A close study is being made of the behaviour and associated body functioning of certain nudibranch species in relation to their coelenterate food. The principal subjects are the dendronotacean *Doto pita* Marcus and the aeolid *Cuthona reflexa* Miller. When searching for a place to settle the veliger seems unaffected by any contact with the tentacles of the thecate hydroid prey: the hydranths of the prey species *Obelia australis* and *Plumularia setacea* retract from the brushing action of the velar cirri and there is little or no nematocyst discharge. Final settlement and metamorphosis is mainly on the hydrocauli. Feeding on the hydroid tissue starts when *Doto* is c250µm long, and both the polyps and coenosarc are attacked. *Doto pita* is principally a suctorial feeder, though it will bite off the prey's tentacles. When *Doto pita* feeds on a polyp, the latter withdraws with little discharge of the nematocysts. In both nudibranch species fluid is actively expressed from the oral glands, the secretion being a mixture of mucus (much less viscid than that of the foot and body) and a protease: there is considerable external digestion of the prey. Suctorial feeding in *Doto* is effected by a pumping pharynx in concert with the periodic enlargement of the digestive cavity: in small *Cuthona reflexa* it is just by ceratal movements. Large *Cuthona reflexa* bite off the hydranths. It does seem, though this study

does not provide conclusive proof, that the mucus reduces considerably the level of nematocyst discharge, outside and inside the nudibranch's body. There is no evidence of a binding function in the stomach, particles of prey circulating freely during the rest of digestion. A protective role for orally produced mucus seems supported by the method of feeding and gland structure shown by the main types of aeolid: the aeolidiids e.g. *Aeolidiella takanosimensis* Baba feed on sea anemones by a combination of dissolution, cutting and pulling, the huge composite oral glands producing mucus for protection and an enzyme for external digestion (dissolution); the glaucids (= facelinids) e.g. *Phidiana militaris* (Alder & Hancock) are rapid biters of hydrozoans, the scattered mucous glands of the oral tube and thick cuticle providing protection — there are no oral digestive glands.

Madreporarian coral and alcyonarian feeding by arminid and eolid opisthobranchs

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Records of opisthobranchs feeding on madreporarian corals are restricted to the aeolids *Phestilla melanobranchia* Bergh on *Tubastrea*, and *Phestilla lugubris* (Bergh, 1870) (= *P. sibogae* Bergh, 1905) on *Porites*. *P. lugubris* and three other opisthobranchs; 2 aeolids and one arminid, are reported living on *Porites* at Dar es Salaam, Tanzania. Adaptations to coral predation are shown in their life histories, ceratal structure and radular morphology. Similarities are suggested to be evidence of convergent evolution rather than close phylogenetic relationship.

Records of aeolid opisthobranchs feeding on alcyonarian or soft corals are also sparse, restricted to *Phyllodesmium* on *Xenia* and related soft corals. Two more species from East Africa and three from eastern Australia, are reported in this paper to be alcyonarian feeders. Ceratal structure and radular morphology are described and show interesting adaptations to their type of feeding.

Both the coral feeders and soft coral feeders are compared with aeolids feeding more normally on hydroids and sea anemones.

The zoogeography of thirty New South Wales opisthobranchs in relation to their larval development

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The zoogeography of thirty New South Wales opisthobranchs, from the three orders Bullomorpha, Nudibranchia and Sacoglossa, is discussed in relation to their mode of larval development. For the thirty species studied: twenty are planktotrophic; four are lecithotrophic; and six are direct developers. Except for eight of the thirty species, the

majority of them appear to have geographic ranges which are explainable in terms of their mode of development. Of those eight species, four are planktotrophic, one is lecithotrophic and three are direct developers. The indirect developing species with dispersal larvae, appear to be restricted to continental Australia. In contrast, the three direct developing species, with non-dispersal larvae, appear to be widespread (i.e. throughout the Tropical Pacific, Pacific, or Indo-West-Pacific). The biology and natural history of these eight species are virtually unknown to give any definite answers as to why these anomalies exist. Possible explanations are discussed which consider: (1) the taxonomic status of a few of these species; (2) the behaviour of the adults of species with non-dispersal larvae; (3) the ability of a species to vary its mode of development in different regions of its geographic range; and (4) some of the biotic and abiotic factors, other than development, which might influence the veliger larvae, causing them to have restricted distributions.

Ecology of sea hares (Aplysiidae) in the Leigh Marine Reserve, North Auckland, New Zealand

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A three-year study has been carried out on an intertidal population of the opisthobranch *Aplysia* (*Varria*) *dactylomela* Rang in Goat Island Bay, Leigh. The species is geared towards an extremely opportunistic life history with short (annual) generation times, high fecundity and long, continuous breeding seasons, high energy conversion efficiency and rapid growth rate. However at this situation *A. dactylomela* seldom has the occasion to exhibit these intrinsic properties. When the annual cycle, in terms of density at different levels across the shore, is followed and related to that of food algae (particularly three species of the rhodophycean genus *Laurencia* which serve as recruitment sites as well as food) it is found that this locality is marginal for the species. Winter storms exert the greatest toll of individuals (90%-95% mortality), but other simultaneous factors leading to the decline of the population are predation, decreasing availability of food and decreasing seawater temperatures. Although densities can be very high at times, it is shown that most individuals are reproductively immature and are likely to die before reproduction. This situation is contrasted with that for a subtidal population of another sea hare *Aplysia* (*Pruvotaplysia*) *parvula* Morch at the same locality. In this population the intrinsic properties of the species are more nearly realized by the individuals.

On the Dimyidae and Plicatulidae — proposed superfamily Plicatulacea

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The Plicatulidae have long been associated with the Spondyliidae in the superfamily Pectinacea. But resemblances are largely confined to cementation by the right valve, the monomyarian condition and, above all, by common possession of secondary, ball and

socket, hinge teeth. This last condition has now been shown to be connected with compression in the transverse plane of the primary ligament. But the Plicatulidae are alone in possessing a secondary (periostracal) ligament while the two differ profoundly in structure of the viscero-pedal mass. Thus both foot and frilled lips occur only in the Spondylidae, identical in these respects with the Pectinidae. Recent work on the Dimyidae⁴ (structure previously almost unknown) has abundantly confirmed earlier evidence^{2,3} indicating fundamental resemblances to the Plicatulidae. There is the same compression transversely of the primary ligament with an elongate dorsally running secondary ligament and some slight development of secondary teeth on an otherwise edentulous hinge. There is a similar absence of foot and frilled lips. As the name indicates, the Dimyidae have two (effectively three) adductors but the anterior one is reduced and conditions in the monomyarian. Plicatulidae may have evolved from something like those in the cemented Dimyidae whereas the Spondylidae clearly evolved with the Pectinidae from byssally attached ancestors. Other features in the Dimyidae, notably the reduced and functionless heart, the remarkably hypertrophied kidneys, loss of cerebropleural ganglia and absence of reflexion in the ctenidial filaments, are all probably associated with their small size and extreme lateral compression. It has been proposed^{2,3,4} that a new superfamily, the Plicatulacea (Dimyacea giving an erroneous impression of structure in the two constituent families) be erected to contain the Dimyidae and Plicatulidae.

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Mode of life and adaptive evolution in the cosmopolitan Triassic bivalve *Monotis*

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Monotis is a generally thin-shelled inequivalved inequilateral radially costate byssiferous bivalve occurring in large numbers in marine strata of Norian age in many parts of the world. Five subgenera have been erected to accommodate the 50-60 taxa covered: *Monotis* s.s. (medium size, subequivalved, fine ribs), *Eomonotis* (small; fine ribs, including on large posterior ear), *Entomonotis* (medium to large, coarse ribs, smaller, smooth ear), *Maorimonotis* (medium to large; thick shelled; coarse to obsolete ribs; reduced ears), *Inflatomonotis* (small; coarse ribs). Despite its abundance, widespread distribution and biostratigraphic importance few attempts have been made to understand its mode of life although some workers have suggested it was epi- or pseudoplanktonic or that it lived attached to seaweed.

Monotis occurs in virtually all marine lithologies but most commonly as shellbeds with fine sand to silt matrix. Its occurrence and morphology suggest it was generally attached throughout its postlarval life to a solid substrate in shallow marine areas with gentle currents

and low to moderate sedimentation rates. But there is no sign of the substrate to which it was attached.

This paper accepts the algal attachment theory and proposes that *Monotis* was epizoic on large algae comparable to modern kelp forests and that different morphotypes occupied different parts of the kelp-like plants and evolved to cope with slightly different environmental conditions. *Eomonotis* may have occupied distal portions of the laminae, with the larger *Entomonotis* on the stipe and less delicate laminae; morphologically aberrant *Maorimonotis* possibly became truly bottom dwelling and endobysate. Periodic storms would tear some plants off the seafloor and these with their epifauna could drift off to other regions allowing *Eomonotis* and *Entomonotis* to achieve their wide distribution as accidentally pseudoplanktonic specimens, some of which continued to reproduce in their new habitat and establish new populations.

Thus evolution would have proceeded from a small, light, subequivalved, possibly epi- or pseudoplanktonic ancestor (e.g. *Otapiria*) to produce firstly *Eomonotis*, then by size increase and ribs coarsening to *Monotis* s.s. and *Entomonotis*, followed by weakening of sculpture and reduction of ears (*Maorimonotis*). Known stratigraphic and geographic ranges support these postulates.

The geography of littoral adaptation in bivalves

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Amongst the bivalves, a number of species occur intertidally. Some, such as the mussel *Mytilus edulis*, are conspicuous because of their epifaunal habit and relatively large size, but many, because of their life habit and/or small size, are much less obvious. To obtain some idea of the success of the bivalves in colonising the littoral zone, total numbers of species and numbers occurring intertidally were estimated.

The total number of bivalve species shows a geographical trend of increase with decrease in latitude. A similar trend is shown in the number of intertidal species. However, when the number of intertidal species is expressed as the proportion of the total fauna, trends are not so obvious or uniform. The proportion of littoral species ranges from 0 to about 47%. Lowest values are found at high latitudes and highest values at middle latitudes, Britain (47% intertidal) in the northern hemisphere and southern Chile (45% intertidal) in the southern. For most other areas the proportion ranges from 15 to 35%.

Values of up to 47% for the proportion of bivalve species which may be found intertidally suggests that, in some areas at least, the bivalves, as a class, have had considerable success in colonising the littoral zone. However, some of these species will be primarily sublittoral although capable of penetrating the littoral zone to a limited degree; others will be truly littoral in the sense that their distribution is mainly in the intertidal zone.

For many areas there is insufficient data to allow these two groups to be distinguished, but such information is available for the British bivalve fauna. It suggests that while 47% of species may be found intertidally, only 25% of these (i.e. about 11.7% of all species) can be considered as truly littoral. If the same relationship is true elsewhere, then for most parts of the world approximately 4-10% of the bivalve fauna can be said to be successfully littorally adapted.

Aspects of the ecology of the giant clams *Tridacna gigas* and *T. derasa*

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On the Great Barrier Reef extensive poaching of giant clam stocks by foreign fishing vessels has occurred for at least the last ten years. Information on catches, their composition and catch per unit effort data were obtained from arrested vessels which probably represent only a small proportion of the total "vessel visits" to the Great Barrier Reef. Surveys were made of "fished" and "unfished" reefs to determine densities of *Tridacna gigas* and *T. derasa*, the two largest and therefore preferred commercial species. Using this information an attempt has been made to assess the magnitude of poaching on existing giant clam populations.

Despite *T. gigas* and *T. derasa* being conspicuous members of the coral reef community surprisingly little is known of their biology and ecology. Several aspects of their ecology are being investigated in permanent study areas established on Michaelmas Reef near Cairns. In one area 2.7 ha, nearly 1,200 giant clams have been tagged, mapped and measured to provide data on habitat preferences and rates of growth, recruitment and natural mortality. Regular sampling of *T. gigas* is being undertaken to determine the reproductive cycle. A report on progress to date will be presented.

Aspects of the biology of *Octopus tetricus*

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O. tetricus is the commonest species of octopus occurring in the waters of south-west Australia. Aquarium studies of growth and food intake have shown that the species grows rapidly under conditions of excess food supply, reaching weights of 2 kg within 6 months. However the rate of growth is directly related to the food intake and it is unlikely that wild individuals achieve such rapid growth.

Males have functional spermatophores when they are about 100-150g in weight while females do not usually lay eggs until they are about 2 kg in weight. However females mate when they are about 500g and the sperm are stored until egg-laying. Females lay up to 700,000 eggs, larger females being more fecund. Embryonic development takes between 22 and 45 days, depending on temperature. The planktonic larvae are 2.5mm long at hatching while newly settled individuals are about 18mm. in total length and weight about 0.3g. Reproduction occurs throughout the year, although there is probably a peak in spring/summer. The lifespan of *O. tetricus* is thought to be about one year.

A quantitative examination of the benthic molluscs of Cockburn Sound, Western Australia

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Thirty stations in Cockburn Sound, Western Australia, were sampled in triplicate with a 0.1m² Van Veen grab. Molluscs were the dominant organisms, constituting 72.19% of all individuals and 89.56% of the biomass. An area of high density and biomass figures was found in the mideastern portion of the deep basin of the Sound. Densities and biomasses outside this area were substantially lower. A comparison of the present results for the central basin with samples made 20 years ago showed no obvious changes which could be attributed to pollution. The seagrass *Posidonia* has disappeared from the eastern shelf in the last 20 years but the causes of this are unknown. This change has been reflected in the molluscs found on the eastern shelf. Two dominant molluscs, *Musculista glaberrima* and *Dosinia incisa*, are recommended for any environmental monitoring programme which might be conducted in Cockburn Sound in the future.

Territoriality in limpets : manipulative experiments and energy budgets

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Territoriality in limpets is now well established and involves the defence of an algal food source against other herbivores, particularly other limpets. This paper is an analysis of the balance between the limpets' requirements and the yield obtainable from the defended area. The approach is two pronged: manipulative field experiments to test the role of limpets in maintaining algal "gardens", coupled with an energy budget approach to balance the energetic needs of the limpet against algal production.

Three examples will be discussed:

1. *Patella compressa* occurs only on the kelp *Ecklonia maxima*, and adults occur singly on the kelp stipe. Experiments show this pattern is maintained by territoriality. Production by the kelp stipe enormously exceeds the requirements of the limpet, so that limitation of food cannot be the reason for territoriality. It is suggested that territoriality minimises damage to the stipe by grazing, hence conserving the plant.
2. *Patella longicosta* defends patches of the alga *Ralfsia expansa*. Juveniles occur singly on the backs of the shells, feeding there on the encrusting *Ralfsia*, but larger animals develop home scars on the rock face, passing through an intermediate stage when they feed on encrusting coralline algae before establishing their own *Ralfsia* gardens. While *P. longicosta* feeds on the corallines, its body weight drops, ash content rises and calorific value and gonad weight declines, suggesting that the food source is inadequate. Experiments show

that territoriality is essential for the maintenance of the gardens. Production by *Ralfsia* closely balances the needs of *P. longicosta*, but declines higher on the shore to the point that it may limit the zonation of *P. longicosta*. Intertidally, more than 90% of *Ralfsia* is maintained in limpet gardens, and the activities of the limpet increase the survival rate and the productivity of *Ralfsia*.

3. *Patella cochlear* occurs in incredibly high densities (up to 1600.m²), juveniles only surviving if they settle on the shells of adults, so that they become stacked on top of each other. Spacing is regular, so that maximum distances are maintained between limpets. Heavy grazing prevents growth of all algae except for the encrusting *Lithophyllum* and a narrow fringe of red alga (*Gelidium micropterum* or *Herposiphonia*) around most of the limpets. Although gut contents comprise almost solely of *Lithophyllum*, production and energy content of this alga are so low that it cannot alone support the energetic needs of *P. cochlear*. The gardens of red algae thus seem vital for the densely packed *P. cochlear*, for although they form only a small fringe around each animal, their production and energy content are high. Limpets which lack gardens have a higher ash content, lower calorific value and lower reproductive output. Experiments show that *G. micropterum* is dependent on the limpet.

Patterns of vertical distribution of intertidal limpets in New South Wales

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During 1975-1978 a study was made of the population biology of a group of common intertidal limpets on shores in the vicinity of Sydney, N.S.W. This group included representatives from the families Fissurellidae, Acmaeidae, Patellidae and Siphonariidae. The two smallest acmaeid limpets are found in restricted habitats on generally sheltered shores; *Patelloida mimula* being found mainly on oyster shells, and *Patelloida mufria* being found on the shells of the intertidal trochid, *Austrocochlea constricta*. Seven species occur on open coastal platforms. *Notoacmea petterdi* is found only on vertical or sloping surfaces at the highest levels on the shore, and the fissurelid, *Montfortula rugosa*, is found only at the lowest regions of the intertidal, or in rock pools. The other five species have overlapping vertical distributions in mid-littoral regions of the shore. The factors influencing the observed patterns of distribution and abundance were investigated for each species, to determine to what extent these five species co-exist, and how such co-existence is maintained or prevented.

It was found that competition for a limited food supply did occur in midlittoral regions of the shore. Experiments involving the caging of limpets in various combinations of species and at various densities, showed that the patellid limpet, *Cellana tramoserica*, was the superior competitor. It was able to cause increased mortality of two acmaeid limpets, *Patelloida alticostata* and *P. latrigrigata*, and of the two siphonarian limpets, *Siphonaria denticulata* and *S. virgulata*.

Observations on the feeding biology of these limpets showed that *Cellana*, with its large docoglossan radula, was able to graze the surface of the rock more efficiently than the other species. Siphonarian limpets are primarily grazers of macroalgae and can only feed effectively when there is some form of algal turf available. In the presence of *Cellana*, such a turf never develops. The smaller acmaeid limpets, although they too feed on microalgae,

have radulae with much smaller teeth than *Cellana*, and apparently cannot get enough food when in the presence of *Cellana*.

Co-existence of the five species in mid-littoral regions of the shore is maintained by several mechanisms. These include the presence of refuges for the smaller species (e.g. *P. latistrigata* can feed effectively amongst barnacles, whereas *Cellana* cannot), behavioural adaptations (e.g. *Siphonaria* can feed on the algal turf that develops on the shells of *Cellana*), and a great deal of variability in the intensity of settlement of juvenile recruits from the plankton. This latter, random effect ensures that high densities of any one species are not attained over the entire shore, nor are they maintained over long periods of time.

Selective site segregation in *Patelloida* (*Chiazacmea*) *pygmaea* (Dunker) and *P. (C.) lampanicola* Habe on a Hong Kong shore

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Hitherto (though originally described as a separate species), *Patelloida* (*Chiazacmea*) *lampanicola* Habe has been regarded as a "form" of *P. (C.) pygmaea* (Dunker). The conical shape of the shell in the former was assumed to result from the settlement and growth of some individuals of the population upon shells of intertidal *Batillaria* (Potamididae).

This study analyses a population of limpets resident upon a small sand flat in Hong Kong and concludes that *P. (C.) lampanicola* Habe is distinct from *P. (C.) pygmaea* (Dunker). This is based upon differences in radula teeth structure, shell morphometrics and behaviour. This study has, moreover, further demonstrated that the earlier confusion surrounding these species results from a very nice example of selective site segregation or resource partitioning. *P. (C.) pygmaea* inhabits stones (in this region of its total range) embedded in the sand but can and occasionally does reside, up to a length of 4.2 mm, upon *Batillaria* shells. Thereafter the flattened form of the limpet shell, on a round substrate presumably makes such individuals more susceptible to either predation or dislodgement. The high-coned *P. (C.) lampanicola*, on the other hand, almost exclusively colonises living *Batillaria* (particularly *B. zonalis*) shells, but can, with little or no significant alteration in form, also colonise stones. *P. (C.) lampanicola* has a positive behavioural response towards *Batillaria* and is clearly living in symbiotic association with the potamidid. The benefits accrued by both are discussed.

Thus, the limited hard shore niche of a primarily soft shore environment (both species are restricted by very low salinities) has been partitioned by these two limpets; one occupies the stones and oyster shells, the other the dense cover of epifaunal potamid snails.

Competition and stability in a guild of limpets

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The Acmaeid limpet *Notoacmea onychitis* co-exists with the pulmonate limpet *Siphonaria kurracheensis* on a vertical rocky shores at Rottnest Island, Western Australia. Experiments in which the relative abundance of these limpets in replicate subpopulations were altered revealed features of the dynamics of the interactions between the limpets.

1. The composition of unaltered control subpopulation changes with time apparently due to yearly differences in recruitment. *Siphonaria* colonizes vacant areas; *Notoacmea* can invade occupied areas.

2. Each species shows evidence of population regulation in which members of the same species affect changes in numbers more than members of the other species, and *Notoacmea* affects *Siphonaria* more than the reverse.

3. The variability in the composition of experimental subpopulations compared to the mean composition of the control subpopulation decreased to pre-manipulation levels after 36 months.

These results add support to the idea that *Notoacmea* is a superior competitor on parts of vertical shore, but indicate that adjustments to disturbances of relative abundances take a relatively long time of three years.

Life-history strategies of five species of intertidal limpet

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The life-history strategies of five species of intertidal limpet, *Cellana tramoserica*, *Notoacmea petterdi*, *Patella peroni*, *Patelloida alticostata*, and *Siphonaria diemenensis*, which occur on the same shore but in different tidal zones, are considered in relation to their different environments. Attention is focussed upon reproductive effort, which is defined as the percentage of assimilated energy devoted to reproduction, and which is measured for each species by using annual energy budgets.

Interspecific differences in reproductive effort appear to be correlated with interspecific differences in rates of extrinsic adult mortality.

Experimental studies of the reproductive strategies of populations of the intertidal limpet *Siphonaria kurracheensis*

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Variations in life history characteristics have been shown to occur between populations of the same species of animals or plants living in different environments. One way of testing if these differences are fixed or plastic is to do reciprocal transplants of populations between environments.

I recorded growth, mortality, total egg output and duration of the breeding season for low and high shore individuals of the pulmonate limpet, *Siphonaria kurracheensis* on both a horizontal and vertical intertidal shore on Rottnest Is., W.A. One year after reciprocally transplanting animals between high and low shore I measured these characteristics.

On both shores I found low populations have a longer breeding season and lower average egg output per individual than high populations. Transplanted animals assumed the same breeding period as animals at the level to which they were transplanted. On the horizontal shore transplanted limpets also changed their average egg output to that of animals already at that level on the shore.

Growth and mortality were not significantly different between low and high populations on the horizontal shore. Low shore animals however grew more during the non-breeding time than the breeding season and experienced higher mortalities during the breeding season than the non-breeding time.

On the vertical shore low animals had a higher mortality during the breeding season than high animals and low shore animals grew more and died more during breeding than non-breeding times. Transplanted animals assumed mortality patterns of animals already at that level on the shore.

Therefore horizontal shore limpets showed differences in reproductive characteristics between low and high populations and these differences were plastic. Vertical shore animals showed differences in both reproductive characteristics and mortalities of low and high shore animals. High shore limpets were plastic in these characteristics but low shore limpets were not.

The influence of grazing by subtidal gastropods on the establishment of furoid algae

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Subtidal reefs in northern New Zealand may support high densities of herbivorous gastropods. These include a limpet *Cellana stellifera*, a turbinid *Cookia sulcata* and a trochid *Trochus viridis*. *Cellana*, *Trochus* and juvenile *Cookia* occupy a range of habitats

but are most abundant on bare rock flats in waters 3-12m in depth. In this habitat their abundance is positively correlated with that of the echinoid *Evechinus chloroticus* which by cleaning macroscopic algae from rock surfaces appears to provide suitable grazing sites for the gastropods.

Field experiments show that mixtures of the above gastropod species may prevent the re-establishment of macroscopic algae in areas from which echinoids have been removed. This paper outlines experiments in which the gastropods are enclosed separately to check the grazing influence of the different species. The results suggest that the grazing activities of *Cellana* and *Trochus* may enhance the establishment of a furoid alga *Sargassum sinclarii*, perhaps by removing ephemerals such as *Ulva*. However, the results are complicated by a caging effect which appears to be independent of the gastropod grazing. General ideas of gastropod grazing will be discussed in the light of these experiments.

The role of grazing by gastropods in the structure of intertidal communities

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On rocky shores in New South Wales there is usually a very abrupt upper limit to distribution of foliose macroalgae. Below this level, in most areas, algae occupy the entire surface of the rocks. Above this level, there are encrusting macroalgae on dry surfaces, foliose algae in pools and some small foliose algae between barnacles. Experiments are described to distinguish between the effects of physical factors (e.g. heat, light) associated with emersion at higher levels on the shore and the effects of grazing gastropods on the upper limit of distribution of algae. Grazing of algal spores by prosobranch gastropods determines the upper limit of foliose algae on the shore. Physical factors determine the biomass of algae in ungrazed areas. The lower limit of microalgal grazers (e.g. the limpet *Cellana tramoserica*) is determined by their inability to feed on macroalgae at lower levels on the shore. The effects of macroalgal grazers (the pulmonate limpets, *Siphonaria* spp.) and of rock-pools are also discussed.

Factors affecting feeding rates of the intertidal carnivorous gastropod *Morula marginalba*

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The intertidal whelk *Morula marginalba* has a more limited distribution than its prey with respect to both height on the shore and intensity of wave action. This is discussed in

relation to the effect of these factors on the rate at which *Morula* kills and eats the barnacle *Tesseropora rosea*.

Study of a tagged natural population of *Morula* provides evidence for seasonal shell growth by this species. Laboratory experiments are described which test for an effect of temperature on *Morula* feeding rate, and for an effect of season on the relationship between feeding rate and temperature. It is suggested that the results of these experiments account, at least in part, for the observed seasonality of growth.

To determine whether there is any basis for expecting *Morula* density to be positively correlated with prey density, field measurements were made on the effect of prey density on the feeding rate of *Morula* on adults and juveniles of a number of prey species. Concurrently with the above experiment, variations in feeding rates were observed in relation to the fortnightly tidal cycle.

The above results are discussed with respect to *Morula* sheltering behaviour and a model of *Morula* distribution is suggested.

A population model of the whelk *Thais orbita*

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A population model of the whelk *Thais orbita* at Fishhook Bay, Rottnest Island in Western Australia has been developed. Data on reproduction, recruitment, growth and mortality were considered in the model. Validation of the model by an experimental manipulation of the population at Fishhook Bay has been attempted. The results of the simulation and their significance will be discussed.

Shore-level size-gradients in *Thais* spp.

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Average body sizes in a variety of marine animals have been reported to be correlated with height in the intertidal zone. However, observations on four species of *Thais* show that the relationship between size-distribution and height (or depth) is highly variable. Intertidal size-gradients in *Thais* have been explained by a size-dependent set of responses to light and gravity, but cage experiments indicate that snails of different sizes behave similarly. It is argued that size-gradients are produced by the direct responses of snails to factors such as shelter, temperature, desiccation and food, and it is suggested that a response to 'token stimuli' is unlikely to evolve when the token stimuli are poorly correlated with the relevant environmental factors, especially if the latter can be monitored directly by the animal.

Food related reproductive strategies in different populations of *Nassarius pauperatus*

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Adjacent populations of *Nassarius pauperatus* differ significantly in how hungry their members are. Females from very hungry populations produce more eggs and egg capsules, but less eggs per capsule, than those from less hungry populations. It was hypothesised that these differences were related to food availability and this was confirmed in a laboratory experiment using two groups from the same population.

Adult mortality and cannibalism of egg capsules are known to increase as food availability decreases and the different reproductive responses to food availability are explainable in terms of these changes. A general hypothesis is also proposed from this work, relating reproductive strategies to dispersive ability.

ABSTRACTS OF POSTERS

On the life-cycle of *Velacumantus australis* (Gastropoda : Potamididae) in the Swan estuary, Western Australia

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Velacumantus australis is the intermediate host of the avian schistosome *Austroilharzia terrigalensis* in the Swan estuary, Western Australia, and aspects of its ecology are being studied as part of an investigation into the epidemiology of this parasite. The longitudinal and vertical distribution patterns of *V. australis* are associated with that of the macrophyte *Halophila ovalis*. *V. australis* is found from the shallows to a depth of approximately 6m but attains its greatest population density between 0.5 and 1.75m. Changes in growth, maturation and population density were documented from monthly, quantitative samples and related to the prevailing temperature and salinity regimes. A generation hatching during the 1976/77 summer grew rapidly until May 1978 when lengthwise growth stopped and did not resume until late spring. The progress of oogenesis and spermatogenesis was assessed from the increasing diameter of developing oocytes, the development of spermatozoa and the changes in the diameter of ovarian and testicular tubules. Gametogenesis corresponded more closely to the rising spring temperature regime than to seasonal fluctuations in salinity. The first evidence of gametogenesis was found in July (\pm 17 months after hatching). The first spermatozoa were found in October 1978 and by November the largest oocytes had attained a diameter of approximately 160 μ m. *V. australis* lives for about 2½ years, breeding during its second summer.

Infection by larval trematodes either obliterates or greatly reduces gonad development. The prevalence of infection increases upstream and near the upstream limit of its distribution in the estuary, up to 67% of the *V. australis* population may be infected.

Studies of muscle metabolism in the marine bivalve mollusc *Tapes watlingi*

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Many studies of the composition of biological tissue and of metabolic reactions therein are hampered by the need to disrupt the tissue in order to identify and quantitate the various metabolites. In recent years nuclear magnetic resonance (NMR) spectroscopy has provided a means of overcoming this problem by virtue of its ability to observe metabolites in intact tissue. Natural-abundance ^{31}P NMR spectroscopy is particularly useful in this respect because it allows the observation of the major phosphorous-containing metabolites, many of which play a central role in metabolism and bioenergetics.

We have examined excised foot and adductor muscle and whole hearts from the marine bivalve mollusc *Tapes watlingi* (the "tapestry cockle") by ^{31}P NMR spectroscopy. The spectra of healthy tissue show prominent resonances from arginine phosphate, AMP, ADP, ATP, sugar phosphates and inorganic phosphates. The fate of these metabolites during tissue ageing has been examined under aerobic and anaerobic conditions and in the presence of various metabolic inhibitors. The position of the inorganic phosphate resonance provides a sensitive monitor of tissue pH. The results of these studies will be compared with similar studies on terrestrial vertebrate tissue.

Energy metabolism of the heart of the mollusc *Tapes watlingi*

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Metabolic inhibitors, anoxia and measurement of oxygen consumption have been used to study the energy metabolism associated with the contractile process of the isolated heart of the bivalve mollusc, *Tapes watlingi*. In this tissue oxidative phosphorylation is used as an energy source for spontaneous contractions, however, if oxygen is removed the tissue is able to metabolise anaerobically and thus maintain near optimal activity. Glycolysis is important in maintaining energy demands for contraction of *T. watlingi* heart, since in aerated medium and in the presence of glycolytic inhibitors the activity gradually decreases to about half the control value. The mollusc heart is more adaptable than mammalian tissue in utilizing alternate metabolic pathways to maintain energy production.

Aspects of the biology of *Gazameda gunni*
(Reeve, 1849) a viviparous mesogastropod and
potential "indicator" of perterbation induced by
sewage pollution.

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Gazameda gunni has a wide distribution on the Continental Shelf off Sydney, N.S.W. inhabiting sandy mud from 55 to 135 metres, with abundance directly related to sand grain size, clay and gravel content of the sediment. *Gazameda gunni* feeds on phytoplankton using specialised ciliary currents and sorting mechanisms which are a modification of the three basic types previously documented for ciliary feeding prosobranchs. The specialised mode of feeding is believed to be related to the brooding of large eggs.

The reproductive system is similar to that of *Turritella communis* in that it consists of an open pallial oviduct. It has, however, a specialised brood pouch which separates the ctenidial complex from the mantle floor. Furthermore, the male reproductive system is similar to that of *Turritella communis*, except that *G. gunni* is a proterandrous hermaphrodite in which the male phase undergoes a brief sexual change which has both male and female anatomical structures. Subsequent to this hermaphroditic phase a female begins and lasts throughout the remaining life. All females in populations of *G. gunni* are reproductively mature.

Embryos are brooded within a brood pouch as an embryonic mass held together by a cylindrical sheath which is attached to the posterior end of the mantle cavity. The egg size at oviposition is relatively large (0.96-1.00mm) compared to other gastropods.

Brooding lasts for a relatively long period (approx. 200 days) until embryos reach 2.6-3.0mm in size and are released as crawling juveniles. The period of development is the longest recorded for a prosobranch.

Oviposition occurs during January in *G. gunni*. The release of metamorphosed juveniles of *G. gunni* occurs during the maximum availability of phytoplankton (August-January) in these waters. It would be advantageous to release juveniles at this period as brooding of large eggs would interfere with feeding.

A significant ($p(0.005)$) linear regression was found between the numbers of eggs and shell size which shows that larger individuals have larger clutches. No relationship was found to exist between shell length and size of eggs, indicating that egg size is constant over size (age).

Quantitative evidence suggests that an increasing gradient of pollution is associated with small egg and clutch size in *G. gunni*. Sewage pollution may reduce the production of oocytes in *G. gunni* by inhibiting feeding by clogging ctenidia.

The reproductive tactic of brooding with a long time of prehatching development is advantageous in that prehatching mortality is nearly non-existent. However, producing a large number of offspring of dispersive type larvae would be advantageous to a local population under conditions of high juvenile mortality induced through environmental stress. Longevity is shortened at polluted sites and this could contribute to local population extinction due to reduction of the number of oocytes produced per female. Further investigation of life history phenomena may show that pollution could greatly increase the

chance of extinction of a local population of *G. gunni* by "interference" with life history tactics. This investigation suggests that a change of reproductive mode or "switch" (e.g. *Crepidula*) is non-adaptive in a local population of *G. gunni* where there is sewage pollution.

Unveiling Australian Ovulids

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Part 1:

A photographic essay establishing how specific living animal patterns and colours of Australian ovulids are true to each species and can be utilised to determine field identification.

Part 2:

Relationships between ovulids and their host alcyonarians, specific or non-specific?

Part 3:

The taxonomic determination of ovulid species utilising radular characteristics, known variations in shell features and geographical distribution.

Multiple haemoglobins in arcid clams

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Many arcid clams possess erythrocytic haemoglobins. The following species of arcids were collected from the waters of Australia and the near Indopacific; *Anadara trapezia* (Deshayes), *Potiarca pilula* (Reeve), *Scapharca gubernaculum* (Reeve), *Tegillarca granosa* (Linne), *Anadara antiquata* (Linne), *Anadara nugax* Iredale and *Anadara passa* Iredale. Their haemoglobins were examined by electrophoresis. Each species possessed two haemoglobins which were present in species specific patterns. The two haemoglobins in each species are genetically controlled at two different loci.

In *Anadara trapezia* a genic polymorphism is displayed by one of the haemoglobins (Hb-2). The usual alleles are Hb-2a and Hb-2b. This polymorphism was present in all of the thirty populations of *A. trapezia* studied. The haemoglobin gene frequencies formed a complex cline; Hb-2a was more common at lower latitudes than Hb-2b which was prevalent at higher latitudes. The oxygen equilibrium curves of Hb-2a and Hb-2b, prepared from homozygous individuals, and Hb-2a + Hb-2b, prepared from heterozygotes, were determined at 15, 20 and 25°C. The curve of Hb-2a was consistently to the right of that of Hb-2b. The curve of the heterozygote was between those of the two homozygotes at 15 and 20°C but at 25°C was almost coincidental with that of the Hb-2a homozygote. This means that at a given temperature animals homozygous for Hb-2a can deliver more oxygen to the tissues for the same amount of cardiac work than can those homozygous for Hb-2b. The advantages of this

to animals living at low latitudes become apparent when it is remembered that the oxygen capacity of water decreases with increasing temperature. Studies on the interaction coefficients of the haemoglobins suggest that the heterozygote has an advantage over both homozygotes at high temperatures.

The lack of polymorphism in the other arcids which were examined is probably related to the relatively stable water temperatures which occur in the tropics for *A. trapezia* was the only species examined whose distribution extends into the cool-temperature region.

Aspects of the biology of *Idiosepius notoides* (Mollusca : Cephalopoda)

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Idiosepius notoides Berry is a small sepioid cephalopod found in the seagrass beds of the Sydney region. It is likely that its distribution extends over much of Australia's subtropical coastline coinciding with the presence of the seagrass beds.

The species is sexually dimorphic and is easily distinguished by its small size and the rugose pad on the surface of the mantle. This pad is used for attachment to the seagrass blades.

Specimens are collected from Careel Bay at monthly intervals, using a fine mesh beam trawl. After fixation in 5% formyl-seawater the animals are sexed, measured and weighed.

Analysis of these data indicates that *I. notoides* is an annual species with a prolonged breeding season extending over the summer months (Oct.-Jan.).

Growth of *Haliotis ruber* in N.S.W.

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A commercial fishery for the blacklip abalone, *Haliotis ruber*, in New South Wales currently yields approximately 400 tonnes of abalone valued at A\$750,000. A program of research aimed at determining appropriate yields for the fishery includes the tagging of abalone to determine growth rates.

Abalone were tagged at 13 sites near 4 major ports, with numbered plastic tags and cyanoacrylate glue. Recoveries to January 1979 numbered 742 representing a recovery rate of 13.5%. Time at liberty varied from 4 weeks to 108 weeks and lengths at recapture varied from 22mm to 133mm.

Recapture data were fitted to the von Bertalanffy growth equation, $L_t = L_{\infty} [1 - \exp(-Kt)]$ where L_t = length at time t .

L_{∞} = average length at which growth ceases

K = rate at which length approaches L_{∞}

The data were fitted using the Fabens method.

Loo's varied from 115mm to 141mm and the respective K values varied from 0.35 to 0.24. Parameters currently being used for yield analysis are $K = 0.43$, $L_{\infty} = 136\text{mm}$.

136mm is less than the mean length in very lightly fished populations and further work is needed to resolve this anomaly. Other work being undertaken includes natural mortality and reef productivity investigations.

Occurrence of interstitial and opisthobranch molluscs on Fijian coral reefs

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Collections of opisthobranchs have been made at five stations from coral reef habitats on Viti Levu. All areas investigated were accessible at low tide by turning chunks of coral or snorkelling over the reef.

Interstitial molluscs recorded from Fiji for the first time include representatives of the order Nudibranchia (*Pseudovermis* sp., *Embletonia* sp.) order Acochliidae (*Hedylopsis* sp., *Microhedyle*) and one species of soleonogaster. The major habitat of the interstitial molluscs is coarse sand pockets on the reef where there is always standing water in the pools and where there is abundant water flow from surge or during tidal change. Another suitable substratum occurs behind the fringing reefs near shore where coarse coral sand is constantly moved by wave action from breaks in the reef or across the reef lagoon.

Larger opisthobranchs including representatives of the orders Nudibranchia, Cephalaspidea, Anaspidea, Notaspidea and Sacoglossa were most commonly found under chunks of dead coral either in small pools near the edge of the reef at low tide or in the rubble zone. They were associated with encrusting growths of hydroids, sponges, algae and bryozoans which are undoubtedly their food sources. Other species appear to live in the reef crevices, as evidenced by the large numbers of crawling forms found on the reef at night.

Species are usually found as single individuals or a low number in any one collection. However, after numerous collections, it is evident that there are common and rare species on the reefs.

Cephalic brood pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda)

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Both *Planaxis sulcata* (Born) and *Fossarus* spp. have a large cephalic brood pouch in the haemocoel in the posterior part of the head. In both genera the pouch appears to be formed

by an epithelial invagination. Its opening to the exterior is a small, slit-like aperture adjacent to the anterior end of the pallial oviduct. Fertilized eggs are deposited in the brood pouch and undergo development to at least the late veliger stage.

The existence of strikingly similar brood pouches in the Planaxidae and Fossaridae suggests that they may have a closer relationship to one another than previously suspected. The freshwater Thiaridae also have a cephalic brood pouch but, unlike the Planaxidae, are parthenogenic.

Stress in estuarine molluscs as measured by adenylate energy charge

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The stress associated with reduced salinity in the gastropod *Pyrazus ebeninus* and the bivalves *Anadara trapezia* and *Saccostrea commercialis* was measured by the adenylate energy charge technique. A statistically significant fall in energy charge occurred in all species when salinity was reduced from 35‰ to 10‰. Mean energy charge values for animals in the low salinity conditions (10‰) were 0.61 for *P. ebeninus*, 0.69 for *A. trapezia* and 0.53 for *S. commercialis*, compared with mean energy charge values in the control animals (35‰) of 0.85 — 0.87 for *P. ebeninus*, 0.84 — 0.85 for *A. trapezia* and 0.64 — 0.76 for *S. commercialis*. The decrease in energy charge occurred within 24h; no further change was found with exposure to low salinity for 48h (*A. trapezia*) or 120h (*P. ebeninus*, *S. commercialis*).

The reduction in energy charge in the three molluscs may have been associated with reliance on anaerobiosis as an indirect result of reduced salinity and, as such, may reflect their relative ability in an unfavourable environment to reduce metabolic demand while using anaerobic processes.

These results were used to examine the value of adenylate energy charge as a biological indicator of the severity of departure from normal environmental conditions.

The genus *Tricolia* (Archaeogastropoda: Phasianellidae) in Australia

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Australian species of *Tricolia* Risso, 1826, have mainly been grouped in the genus *Pellax* Finlay, 1927, but Ponder (1965) has shown that the type-species of the latter is a mesogastropod (an eatoniellid) and is thus unrelated.

There are six species of *Tricolia* in Australia, four of them endemic. Judging by shell and radular characters, the Australian species closest to *Tricolia*, s.s., of Europe is *T. fordiana*

(Pilsbry, 1888), which ranges from the Persian Gulf to Western Australia and Queensland (it has not yet been recorded in the literature from Australia but is an abundant minute species). *T. tomlini* (Gatliff & Gabriel, 1921) is a southwestern Australian endemic, while *T. gabiniana* (Cotton & Godfrey, 1938) is endemic to southwestern and southern Australia (east to South Australia). In life, both commonly have a bryozoan epizoic on the shell. *T. rosea* (Angas, 1867) is endemic to all of southern Australia. Judging by its large first shell whorl and the enlarged aperture of the presumed female, there may be ovoviviparity. *T. tomlini* and *T. rosea* have radulae with a narrow central tooth between the two innermost laterals. In the subgenus *Hiloea* Pilsbry, 1917, this trend leads to fusion of the innermost pair of laterals into a pseudocentral. *Hiloea* has both shells and radulae that are sexually dimorphic, and in Australia is represented by *T. (H.) virgo* (Angas, 1867) in New South Wales and Western Australia, and *T. (H.) variabilis* (Pease, 1860-61), a widespread Indo-Pacific species occurring in Queensland (not yet recorded in the literature).

Pellax johnstoni Cotton, 1945, of southwestern Australia, may be a true *Pellax*.

A major conclusion of the study (which considers all the Indo-Pacific species) is that the shell features of *Tricolia* are evolutionarily conservative while the radulae are plastic. Erection of subgenera and genera based solely on radular characters is therefore not advised. Studies of the living animals are much needed.

Embryology of three N.S.W. Opisthobranchia

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A poster display will depict the major embryonic events in the development of three nudibranchs. Each species will represent one of the three types of development found among local fauna. Planktotrophic development (Type 1) will be represented by *Dendrodoris nigra*. For this species two larval forms will be shown. Lecithotrophic development (Type 2) will be illustrated by *Hoplodoris nodulosa* and direct development (Type 3) will be represented by *Rostanga arbutus*.

On the ultrastructure and histochemistry of the digestive gland of *Oncomelania hupensis quadrasi* (Hydrobiidae)

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This amphibious prosobranch from the Phillipines is an intermediate host of the human schistosome, *Schistosoma japonicum*. The parasite matures in the connective tissue and haemocoelic spaces around the digestive gland of the snail. An examination of the

ultrastructure of the digestive tissue of healthy, uninfected snails has been undertaken prior to investigation of the effects of parasitism on the gland.

The digestive gland of *O. h. quadrasi* occupies the posterior region of the visceral mass, where it is mingled with the gonad. It consists of two unequal lobes of a compound tubular or acinar nature, connected to the stomach by a central duct which opens near the oesophageal entrance.

The gland ducts are lined with a columnar ciliated epithelium, whilst the lobules of the gland consist of three types of cells here described as the digestive cell, the secretory cell and the narrow cell. In previous light microscope studies of prosobranchs these three types have been described and in some cases a fourth type, the calciferous cell, was reported. Work on pulmonates also described a mucous cell, which has not been found in prosobranchs.

The digestive cell is a columnar cell which appears to go through various morphological changes throughout its life. It has a dense brush border of microvilli along the apex, which assists in its main function, the absorption and digestion of food material from the lumen of the gland. The characteristic appearance of organelles such as the poorly developed Golgi apparatus and endoplasmic reticulum and small dense mitochondria, can be seen at all functional stages of the cell.

The secretory cell is conical in shape and is characterized by a well developed granular endoplasmic reticulum and Golgi apparatus involved in the production of zymogen granules. Most secretory cells in addition contain an electron dense aggregate that, by means of electron microprobe analysis, has been shown to contain calcium. This dense aggregate is eventually released into the lumen of the gland. The secretory cell in *Oncomelania* therefore combines, to some extent, the characteristics of the calcium cell and the excretory cell as described for some terrestrial pulmonates.

The narrow cell, described in other snails as an undifferentiated cell, resembles the flagellate cell of some prosobranchs. The presence of numerous parallel microtubules suggests a special function, e.g. structural, locomotory or sensory.

At the base of the gland epithelium cellular processes and occasional small cells are found that contain a number of small, (approximately 100nm diameter) electron dense granules. These could represent parts of endocrine cells or possibly aminergic nerve terminals; the latter suggestion being supported by the presence of microtubules in some of these processes.

Osmotic regulation and respiration in a marine pulmonate mollusc

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Amphibola crenata, a common air-breathing gastropod mollusc on mud flats exposed to wide variations in salinity, survives for many days in the laboratory in diluted and in concentrated seawater. In the range of 25% — 125% seawater, the osmotic concentration of the blood is ca 50 mOsm above that of the external medium and, in fresh water, is maintained at ca 280 mOsm. Equilibrium is achieved within ca 6 h of exposure to the

experimental medium. The volume of intracellular water, however, increases in diluted media (x 2.5 in 25% seawater after 6 h) and decreases in hypertonic media. Complete cell volume regulation is accomplished after 6 h in 50% seawater, but is still incomplete after 9 days in 25% seawater. Intracellular volume is more easily adjusted in diluted media than in moderately hypertonic media (e.g. 125% seawater).

Oxygen consumption was related to body weight by the equation $VO^2 = aW^b$. The slopes (b) of the log-log plots relating body size to oxygen consumption ranged from 0.43 — 0.46 and the 'proportionality factor' (a) ranged from 0.108 — 0.158 over the range 0-125% seawater. Oxygen consumption was not significantly affected by salinity. There is no significant difference between aerial and aquatic oxygen consumption. During exposure to declining oxygen tensions the snails were found to be oxygen independent, the degree of independence increasing with decreasing salinity. During exposure to anaerobic conditions the snails were found to build up an 'oxygen debt' which was subsequently 'repaid' upon return to aerated seawater. The oxygen debt reached a maximum after 6 hours hypoxia over the range 0-125% seawater. Small individuals with high metabolic rate are less independent of the ambient oxygen tension than larger individuals.

Uptake and Loss of Radium-226 in the Freshwater Mussel *Velesunio angasi*

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Velesunio angasi occurs abundantly in the aquatic environments in the vicinity of the uranium deposits in the Magela Creek system, Northern Territory. This mussel is a dietary component of the Aboriginal inhabitants. When mining begins it is expected that the levels of water-borne radium will increase. This study aims to obtain experimental data on the uptake and loss of radium — 226 in *Velesunio angasi*. Such data will allow the calculation of the level of radium — 226 in the mussel flesh for a known exposure time, radium concentration and certain other chemical parameters. Hence the potential dose to the Aboriginal consumers can be determined.

Aspects of the animal's biology that are likely to affect the levels of radium — 226 are also being investigated.

Samples of water, sediment and mussels have been collected for evaluation of base-line radium — 226 concentrations in a number of areas. Preliminary experiments have investigated.

- (i) the approximate rates of uptake and loss of radium — 226 by mussels
- (ii) losses of radium during the experiment (e.g. onto tank walls)
- (iii) variation in radium — 226 levels in water, food, mussel flesh and shell
- (iv) problems encountered in the use of mussels in laboratory experiments
- (v) loss of radium from mussels with high natural levels held in radium free water

Non-marine molluscs of S.E. Australia

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South-eastern Australia, consisting of Victoria, Tasmania and the parts of New South Wales and South Australia south of the 33°S parallel, constitutes a faunal region, the Peronian. Australia can be divided into six such regions, each with its own non-marine mollusc fauna. Each region is dominated by a different group of molluscs, showing a wide species radiation and a high proportion of endemism.

The non-marine mollusc fauna of South-eastern Australia consists of 39 families and about 210 species. The main families are the Hydrobiidae, Planorbidae, Rhytididae, Charopidae and Hyriidae. The Charopidae, with 54 species, is the dominant group for the Peronian region.

Examples of the variation and distribution within these groups are shown.

Factors influencing production of the cockle *Chione stutchburyi* in the Avon-Heathcote estuary, Christchurch, New Zealand

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The distribution (number m^{-2}) of the cockle *Chione stutchburyi* (Wood, 1828) in the Avon-Heathcote estuary, Christchurch, New Zealand (43°33'S, 172°44'E) is presented based on 200 quantitative sample sites. Relationships between total shell length, ash-free dry weight and age of 1000 individuals from a variety of growth conditions are discussed and are used to estimate the spatial distribution of *Chione* biomass (g ash-free dry wt m^{-2}) and production (g ash-free dry wt $m^{-2} yr^{-1}$).

The distribution of density, biomass and production are discussed in relation to the physical parameters of sediment composition (% mud, mean and median grain diameter of the sand fraction, and degree of sorting) and tidal position in an attempt to identify factors responsible for distribution and influencing production.

Consideration of each factor on two levels was found necessary. First, *Chione* tolerance limits to each factor were established on a "presence/absence" basis, thus defining the zone of intolerance. Second, using stations in which none of the factors are limiting, *Chione* preference to each factor was established, within the zone of tolerance, or regulation, based upon a peak in number, biomass and production.

Chione distribution was found to be restricted to below EHWN and to sediments with less than 50% mud and a mean particle diameter of the sand fraction smaller than 2.25 ϕ .

Sex in *Potamopyrgus*

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1. Introduction: It is accepted that in bisexual populations natural selection will keep the sex ratio to 1:1. Where parthenogenesis occurs alongside sex, the situation will be very different and it could be expected that the sex-ratio established would reflect the balance of advantage between sexual and non-sexual reproduction.

This poster presents for discussion observations on sex-ratios in natural and laboratory bred populations of the parthenogenetic hydrobiid *Potamopyrgus* from Europe, Australia and New Zealand, but interpretation is still not clear.

2. Natural Populations: A comparative table was presented of the percentage of males in populations sampled in the three areas. An Air photograph shows a small watershed in New Zealand that has been sampled for 9 years and gives yearly averages for males in neighbouring streams. This illustrates both the wide differences found even in similar habitats and the persistence of these from year to year.

3. Laboratory breeding: Females from the three areas have been kept alone or with males from their own or other regions. Sex-ratios found in the young bred have not always been the same as in the parent population(s). Figures are presented which suggest the following very tentative conclusions and interpretations:

A. Females held alone: generally produce daughters by parthenogenesis. Very few males have appeared but some at least may have been the result of prolonged sperm storage and/or embryonic diapause. One New Zealand locality has females showing little parthenogenesis.

B. Females held with males: generally also produce daughters, and present evidence suggests that these too are parthenogenetic, most captive males losing their fertility. Exceptions are the one N.Z. locality mentioned above, young from mated groups including many males. In another case where inherited colour gives evidence of paternity the young are largely male.

The significance of these findings for natural situations is not clear.

INSTRUCTIONS TO AUTHORS

Papers received prior to October 1st in any year will be considered for publication in the issue for the following year.

1. Papers submitted for publication should be prepared with due regard to the current issue of the *Journal*. All papers will be reviewed by two referees before acceptance by the Editor, and upon acceptance, all copyrights become the property of the Society.

2. Manuscripts, two copies of which must be submitted, should be double-spaced type-written on one side only of the paper, leaving top and left margins at least 3 cm wide. Author's name and address or institution should appear underneath the title. A summary should be included. Literary amendments necessary for the standard of uniformity of articles published in the *Journal* will only be made at the discretion of the Editor. Latin names of genera and species, and titles of periodicals and books should be underlined, but nothing else. Symbols and abbreviations should conform with those recommended in the Royal Society's *General Notes on the Preparation of Scientific Papers* (London, Cambridge University Press, 1950).

3. Text figures should be drawn with black indian ink on Bristol board, of such size that they can be reduced satisfactorily to a maximum width of 14 cm. Photographs for reproduction as half-tone plates should be unmounted, glossy prints showing good detail and moderate contrast; full plate size will be 22 cm by 14 cm.

4. References should be listed alphabetically at the end of the paper, in the form:

BURN, R., and M. C. MILLER, 1969. A new genus, *Caldukia*, and an extended description of the type species, *Proctonotus ? affinis* Burn, 1958. *J. Malac. Soc. Aust.*, 1 (12): 23 - 31, pl. 2.

Titles of periodicals should be abbreviated according to the *World List of Scientific Periodicals* (4th ed., Butterworth), except that capital initial letters are used throughout. In the text, references should be cited with the year of publication, e.g. Burn and Miller (1969), or if to a particular page (Gerrard, 1966: 7).

5. Papers describing new species and subspecies will not be accepted for publication unless the primary type material is deposited in a recognized public museum, and the museum registration numbers of the type material quoted. It is suggested that at least part of the type material of any new species described from Australia or its seas be deposited in an Australian museum. Type localities should be defined as accurately as possible.

6. Experimental papers dealing with ecological, physiological, histological and cytological matters must cite repository and registration numbers, and locality data of voucher specimens, either in the text or in an appendix.

7. Galley-proofs will be sent to authors who should return them with the least possible delay. Only the minimum of essential corrections should be made.

8. Reprints may be purchased at cost price if ordered when galley-proofs are returned.

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